

PADS, FURROWS
AND PAPILLAE
IN THE FOOT
OF BIRDS

Ingvar Lennerstedt

Lund 1973

Pads, furrows, and papillae in the foot of birds

INGVAR LENNERSTEDT

CONTENTS

I.	Introduction	1
II.	Development of furrows, pads, and papillae in domestic fowl	6
III.	Pads and folds in European passerine species	21
IV.	Pads and papillae in nine passerine species	39
V.	Pads and folds in species with zygodactyle feet	54
VI.	A functional study on papillae and pads in passerines, parrots, and owls	62
VII.	Comparative morphology of pads and folds	81
VIII.	Seasonal variation in papillae of Wood Pigeon, Pheasant, and House Sparrow	99

I. Introduction

The feet of birds show an impressive variation in structure. This is related to the highly different ways of living. The variation in the foot structure engaged many ornithologists in the nineteenth century, when the typological species concept was commonly embraced, and the classification used one or only few anatomical details. The different classifications were reviewed by Gadow (1893). The anatomy of the legs and the bill play a more or less important role with the different authors. Cabanis in 1847 classified from features principally in the locomotor apparatus and particularly from the tarsal scutellation and the number of flight and tail feathers.

Reichenow (1871) arranged the birds solely according to the leg anatomy; he used the number, position, and form (Gestalt) of the digits; the structure of the claws including the comb of digit III; and the tarsal scutellation.

Reichenow argued that it is possible from the leg anatomy to determine the systematic position of a bird at any level: family, genus, and sometimes even species and sex; it is also possible to recognize the way of living and feeding. This idealistic species concept was successively replaced by a population concept with the theory of organic evolution, due to gene mutations and natural selection, as the basic idea. In relation to this change, the studies on the structure of the scales and the direction of the digits diminished. A recent treatment is made by Bock & Miller (1959). The hind leg anatomy, none the less, attracted great interest because of the adaptations for different ways of living and the use of certain muscles in the classification. There are many descriptions and comparisons of muscles and skeletal elements; the extensive literature was reviewed by Hudson (1937) and George & Berger (1966). Numerical taxonomic methods were applied on the leg muscles of certain charadriiform and galliform birds by Hudson et al. (1966) and Hudson et al. (1969), and principally functional approaches by, among others, Stolpe (1932) and Cracraft (1971).

The extensive literature and knowledge on the scales and muscles greatly contrasts with the sparse literature on pads, furrows, and papillae in the plantar surface of the foot. The plantar skin has been almost completely overlooked both in older and recent reviews on bird skin. Karl Georg Wingstrand in 1960 directed my attention to these structures and the few and vague descriptions of pads and papillae. He also showed me the paper by Madsen & Wingstrand (1959). I then began work on the present thesis.

My first task was to gather birds of different families and fix the feet. For this collection, I got valuable help from a large number of ornithological friends, who were amply supplied with fixatives; I also got a great many fixed feet from the bird banding stations at Ottenby and Falsterbo. The basic approach was descriptive and comparative on the gross morphology of pads and the microscopic anatomy of papillae in the whole avian class. But the subject soon became too vast and had to be broken down into minor projects. The collection of material was then directed to the particular problems.

The material of Passeriformes greatly outnumbered that of the non-Passeriformes; therefore I concentrated my attention on the Passeriformes. I was first bewildered by the individual variation in the occurrence of furrows. When I related the pads and folds to the phalanges and joints, however, it was possible to deduce a basic pattern of pads and folds in the examined Passeriformes and to correlate the pattern with the arboreal habits (Chapter III).

In certain closely related species of Passeriformes, I saw minor differences in size of pads and in number and size of papillae. Therefore, I chose three tit species and six warbler species and compared them in detail (Chapter IV).



The differences are possibly adaptations to the substrate. But little is known about the thickness and the surface structure of the twigs that the birds frequent, although clear differences have been observed in the habitat of the three tit species coexisting in European broad-leaved woods.

The study on the individual variation in the species of Passeriformes (Chapter III) and the study on the differences between closely related species (Chapter IV) demanded knowledge on the development of pads, folds, furrows, and papillae in the embryo. As subject for this study, I chose the domestic fowl, although it lacks folds. The results are presented first in the thesis (Chapter II).

Parallel with the study on the Passeriformes, I compared the species of non-Passeriformes, although there was much less material; the number of species in the Scandinavian fauna is restricted. The birds with zygodactyle feet have attracted particular attention since the studies by Steinbacher (1935) and Bock & Miller (1959). The posteriorly directed digit IV is regarded as an adaptation for perching. I studied the pads, folds, and furrows in species representatives of woodpeckers, cuckoos, and parrots (Chapter V). The pads in the parrots differ fundamentally from those in the other species; this is clearly related to the different way of living.

The next step was a functional study of the attachment of the pads to the phalanges, joint capsules, tendon sheaths, and tendons in birds with clearly different living habits. I chose a crow, a parrot, and an owl. I also studied the microscopic anatomy of the papillae. The digits, pads, and papillae were manipulated in various ways with pins and tweezers. Chapter VI reports this study. The findings could explain the differences in the morphology between the parrots and the other species with zygodactyle feet.

There then still remained the comparative morphology of pads and folds in different families and orders of birds. Chapter VII describes eighteen species and together with the descriptions in the earlier chapters, I made a comparative survey. The functional interpretations were first considered. The exclusively terrestrial species has a tendency to reduce the number of pads by fusions. The arboreal species living on thin branches have folds at the joints, whereas other arboreal species have pads at the joints. This led to the conclusion that the folds at the joints are reduced pads. After these functional interpretations, I deduced a basic pattern of pads in the avian class, related to arboreal habits.

When I examined the papillae in the species of Passeriformes, I saw that the structure of the papillae changed by season. Later, I had the opportunity to study a large material of Pheasants and Wood Pigeons, collected for other investigations by my colleagues at the institute, and I could treat this subject

in detail (Chapter VIII). The seasonal variation in papilla structure is a physiological adaptation and has the probable function in the thermoregulation of the body and the leg.

Acknowledgements

Most of my study was done at the Department of Structural Zoology, University of Lund. I am greatly indebted to Professor Erik Dahl, head of the department, both for the laboratory facilities and for many discussions and valuable advice, which made the present study possible. I also thank Professor Karl Georg Wingstrand at the University of Copenhagen for introducing me to the subject, for comments on manuscripts at various stages in the study, for the supply of histological slides of plantar skin, and for the supply with fixed material of three species that had lived in the Zoological Gardens in Copenhagen. Most work on embryology was carried out during one year as lector at the Zoological Institute at the University of Gothenburg, and I am grateful to Professor Anders Enemar for the working facilities in the laboratory. I have discussed many problems with several colleagues at the Zoological Institute in Lund, and I thank Dr Börje Karlsson, Dr Harry E. Myhrberg, and Dr D.F. Owen for comments on particular parts of the thesis. My thanks go also to Dr Gustaf Rudebeck at the Zoological Museum in Lund and Dr J. Lepiksaar at the Museum of Natural History in Gothenburg for the supply of skins; to Miss Lena Bolander, Miss Eva Olsson, Miss Kristina Larsson, Mrs Lena Eriksson, and Miss Ulla Edland who assisted in the histological work; also to Mrs Lena Eriksson and Mr Mats Lind who prepared most of the illustrations and to Mrs Cynthia O'Brian who drew the figures 12-16 in Chapter II. My thanks to the large number of ornithologists who collected birds and fixed the feet. I am indebted to the Swedish Ornithological Society for the material collected by the ringing staff at the bird stations Ottenby and Falsterbo. The material of Pheasants and Wood Pigeons was collected under the management of Dr Håkan Stenram and Dr Lars Ljunggren, and I am grateful to them for the ample supply of material, Dr Lars Ljunggren also for his observations on the histological conditions in the internal organs. Thanks also to Dr Sven Mathiasson for the collection of birds and fixation of feet during visits in Sudan. Dr Peter Vorwerk gave valuable advice in the statistical treatments of figures in Chapter III and VII. Mr W.F. Salisbury corrected the English manuscripts. Mr Lajos Erdös made most of the photographic work. Mrs Inga-Lis Svensson typed the final manuscript and Dr Lennart Cederholm at Zoo-Tax Offset printed the thesis. Finally, I wish to express my gratitude to my wife Kerstin

Lennerstedt, my father Gustaf Lennerstedt, and my late mother Sigrid Lennerstedt for the patient encouragement and support during the many years of investigation. The investigation was sponsored by fellowships for the licentiate and doctor degrees of examination. Financial support for the laboratory work was supplied by grants from the University of Lund, the Physiographic Society of Lund, and the Swedish Society for Sciences.

References

- Bock, W.J. & Miller, W. DeW. 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. - Amer. Mus. Novitates 1931:1-45.
- Cracraft, J. 1971. The functional morphology of the hind limb of the domestic pigeon Columba livia. - Bull. Amer. Mus. Natur. Hist. 114:171-268.
- Gadow, H. 1893. Vögel. II. Systematischer Theil. In: H.G. Bronn's Klassen und Ordnungen des Thier-Reichs. Band VI, Abt. 4. C.F. Winter, Leipzig.
- George, J.C. & Berger A.J. 1966. Avian myology. Academic Press, New York & London.
- Hudson, G.E. 1937. Studies on the muscles of the pelvic appendage in birds. - Amer. Midland Natur. 18:1-108.
- Hudson, G.E., Hoff, K.M., Berger, J.V. & Trivette, E.C. 1969. A numerical study of the wing and leg muscles of Lari and Alcae. - Ibis 111:459-524.
- Hudson, G.E., Parker, R.A., Van den Berge, J., & Lanzilotti, P.J. 1966. A numerical analysis of the modifications of the appendicular muscles in various genera of gallinaceous birds. - Amer. Midland Natur. 76:1-73.
- Madsen, H. & Wingstrand, K.G. 1959. Some behavioural reactions and structures enabling birds to endure winter frost in arctic regions. - Vidensk. Meddel. Dansk Naturh. Foren. 120:15-23.
- Stolpe, M. 1932. Physiologisch-anatomische Untersuchungen über die hintere Extremität der Vögel. - J. Ornithol. 80:161-246.
- Reichenow, A. 1871. Die Fussbildung der Vögel. - J. Ornithol. 19:401-458.

II. Development of pads, papillae, and furrows in the foot of domestic fowl.

ABSTRACT

The morphological development of furrows, pads, and papillae in the plantar part of the chick embryo foot is described. The furrows develop through two stages: the furrow rudiment and the early furrow stage. The skin in the furrow rudiment has thickened epidermis and hinges inwards by a change in form of basal epidermal cells. In the early furrow stage, the epidermis grows deeper in skin by proliferation of epidermal cells. The different furrows in plantar surface reach the early furrow stage by ten to twelve days of incubation. Certain furrows are subject to individual variation, which depend either on a furrow failing to develop, or on one or two furrows subdividing a pad and appearing in different sites of that pad.

The pad develops through two stages: the pad bud and the early pad stage. The transition is indicated by the development of the limiting furrows to the early furrow stage. The bulging of the pad depends in part on proliferation in subepidermal mesenchyme and in part on increase in intercellular substance. By eleven days of incubation, the subepidermal mesenchyme is differentiated into dermis and subcutis.

The papilla develops through three stages: the papilla rudiment, the papilla bud, and the early papilla stage. The first papillae appear in the middle of the pad as an epidermal placode and a dermal condensation, which are comparable to those in feathers and scales but smaller. New papillae appear peripherally to the one first established. The time for development of skin to papilla bud in the different pads is described and related to function.

CONTENTS

Introduction

Material and methods

Results

Terminology of embryonic structures

Designation of pads

Individual variation in furrows and pads

Development of furrows and pads

Nine days

Ten days

Eleven days

Twelve days

Times for development of furrows
Development of papillae
Times for development of papillae
Discussion
Literature

INTRODUCTION

The morphogenesis of feathers and scales depend on interaction between epidermis and dermis, in which the dermis acquires control over the differentiation of the epidermis when in contact with it. Since this was shown by Sengel (1958), Wessels (1962), and Rawles (1963), these epidermal structures have been extensively used in experimental studies (for review, see Cohen 1966, 1969, Sengel 1971). The collagen fibres in the dermis have also been proposed to play an important role in feather morphogenesis (Stuart & Moscana 1967, Goetinck & Sekellick 1972). The morphogenesis of scales on the frontal side of the shank was examined by Wessels (1961, 1962), Thomson (1964), and Sawyer (1972a, 1972b), and the mitotic pattern in the developing scales by Yohro (1969).

The plantar surface of the foot is occupied by a number of pads, separated by furrows. The pads are furnished with papillae sometimes characterized as small scales, but they differ from scales in the structure of the horny layer and therefore are properly designated papillae. Although dermo-epidermal recombination experiments with rudiments of papillae, scales, and feathers have been performed (Sengel & Patou 1969, Linsenmeyer 1972), there is no study specially devoted to the development of furrows, pads, and papillae.

In their description of the chick embryo stages, Hamburger & Hamilton (1951) use diagnostic characters in the limb. They state that, by 11 days of incubation, the pads are conspicuous; by 12 days, the surface of the major pad is ridged; by 13 days, the papillae are visible on the major pads; and by 14 days, the entire plantar surface is covered with papillae. The development of pads, furrows, and papillae in the foot occurs at late stages compared with the development of feathers, the first of which are visible as rudiments on the dorsal apterium after about 6,5 days of incubation (Sengel 1964). The present study describes the development of furrows, pads, and papillae, and gives the time for their appearance in different part of the foot in the chick embryo.

MATERIAL AND METHODS

The eggs were incubated at about 37,5°C and the developmental stage determined

according to Hamburger & Hamilton (1951) series. When in the present study embryos are mentioned by days of incubation, this means that they have been examined concerning stage in the Hamburger & Hamilton series. Table I shows the number of embryos studied in histological preparations. By fourteen and sixteen days of incubation, the digits were treated separately in sagittal sectioning.

The histological routine comprised fixation in Bouin, embedding and sectioning in paraffin at 7 μ m, staining in Ehrlich's haematoxylin, and mounting. Embryos of different ages were treated with colchicine, which was diluted to 1:10⁴ or 1:10⁵. The colchicine solution was administered to the amnion cavity or to the inner wall of the air chamber in an amount adjusted to the size of the embryo and the concentration of colchicine, from 0.05 to 1 ml. The treated embryos were fixed in Carnoy and stained in Gomori's haematoxylin (Melander & Wingstrand 1953). The purpose was to arrest mitoses and localize centres of mitotic activity, but the treatment was successful only in few embryos aged nine to eleven days.

At each stage of development, the feet of 10-20 embryos were fixed and the development of pads, furrows, and papillae were examined through a binocular microscope. The individual variation in the occurrence of furrows was studied in 200 one-day chicks of the Kath-line race.

The height of epidermal cells was measured by means of a micrometer scale in the ocular lens of a microscope. The range of variation was determined from at least five embryos of each stage. The dermal cells were counted by means of a grid in the ocular lens and 800x microscopic magnification. In the calculation of dermal cell density, the number of cells was multiplied with a constant for the thickness of the histological preparation, 7 μ m.

RESULTS

Terminology of embryonic structures

The diagrams in Fig. 1 show the stages in the development of a furrow, a pad, and a papilla. The drawings are used as reference during the histological and morphological descriptions. The following terminology is used to describe the developmental stages.

Furrow rudiment: a thickened epidermis with flat or inward-curved surface.

Early furrow stage: a thickened epidermis with surface hinged inwards, forming a score; as seen in sagittal section, the surface in the score forms an acute angle.

Pad bud: a bulging of skin, delimited by furrow rudiments.

Early pad stage: a bulging of skin, delimited by furrows.

Papilla rudiment: a dermal condensation and an overlying epidermal placode; no measurable outgrowth.

Papilla bud: a dermal papilla and an epidermal outgrowth with measurable length; as seen in section, the epidermal surface at the margin forms an obtuse angle.
Early papilla stage: a dermal papilla and an epidermal outgrowth; as seen in section, the epidermal surface at the margin forms an acute angle.

The words "furrow", "pad", and "papilla" are used when no precise stage is meant.

Designation of pads

The pads are situated either at a phalanx or at a joint between phalanges; therefore they are referred to as phalanx pads or joint pads. The designation of pads is properly made in accordance with that of the phalanges.

The designation of phalanges is usually made in a distal sequence (cf. George & Berger 1966). In the present study, a proximal sequence is adopted so that the distal phalanx, carrying the claw, is given number 1, and the proximal phalanx number 2, 3, 4, and 5 in the respective digit (Fig. 2). The distal phalanx of digit I is thus phalanx I:1 and the proximal phalanx is phalanx I:2. The Roman numeral refers to the digit, and the Arabic numeral to the phalanx. The joints between phalanges are designated according to the participating phalanges. The middle joint of digit II, for instance, is joint II:2/3; the numerals of phalanges are separated by an oblique stroke.

The pads are designated according to the adjacent phalanx or joint between phalanges, as shown in Fig. 3. For instance, the two phalanx pads in digit I are designated pad I:1 and pad I:2, the joint in the middle of digit II is designated pad II:2/3. Some phalanx pads are subdivided by furrows. For instance, pad II:2 has two pads, the distal pad II:2 and the proximal pad II:2. The pad ventral to the trochleas of tarsometatarsus is designated the central pad.

The proximal sequence of pad designation was adopted after a comparative survey of pads in birds of different orders. The distal pads of a digit are always easily recognized and related to phalanx or joint, whereas the circumstances at the base of the digits are less evident. Therefore the scrutiny for examination of pads and furrows in a digit started with the pad of the claw and continued with the other pads in proximal sequence.

Individual variation in furrows and pads

A furrow present in one individual may be absent in another. This individual variation was studied in 200 newly hatched chicks.

The digit is divided into regions in which there is a variation. The types in each region - one, two, or three pads depending on the number of furrows - are shown in the diagrams in Fig. 4. The percentual occurrence of each type is indicated.

Pad II:2 is subdivided into two pads in 84 per cent of the chicks, but one pad or three pads occur in a minor number. A similar variation occurs in pad III:2

Pad II:3 is subdivided into two or three pads. Distal pad II:3 has the same size in the examined birds, and proximal pad II:3 is subdivided in 93 per cent.

Ventral to phalanx III:4, there are one, two, or three furrows. About half the number of chicks have one furrow separating distal pad III:4 from central pad, which then extends to the middle of phalanx III:4. Two furrows at phalanx III:4 occur in about one-third of the chicks and three furrows in eight per cent. The distal pad III:4 is always the same size, whereas central pad is reduced in size when there are two or three furrows. When only one furrow occurs, the central pad is considered to have fused with skin that in other chicks develop to the proximal pad III:4.

Pad IV:5 occupies only a minor part of the area ventral to phalanx IV:5. The adjacent joint pad, pad IV:4/5, is comparatively large. Pad IV:5 is undivided in about two-third of the chicks and subdivided in about one-third.

The variation in pad structure at joint IV:2/3 and phalanx IV:3 has a different character. In 22 per cent of the chicks, there is one furrow that divides the skin into one joint pad and one phalanx pad, which are designated pad IV:2/3 and pad IV:3, respectively. In 78 per cent, this furrow is absent, and the two pads have fused to one large pad ventral to both the joint and the phalanx. The interpretation of the large pad in the three-fourths of the chicks as a fusion of two pads is supported by the circumstance in the pheasant, Phasianus colchicus, which always has two pads separated by a furrow (own observations).

The variation in pads at joint IV:3/4 and phalanx IV:4 is comparable to that at joint IV:2/3 and phalanx IV:3. The furrow separating pad IV:3/4 and pad IV:4 is present in the same frequency, about one-fourth of the chicks.

Development of furrows and pads

The development of the foot of six through twelve days of incubation is shown by diagrams at the same magnification in Fig. 5. At six days, the proximal part of the limb bud is more narrow than the distal part, which is flattened to a foot plate; a limb paddle has been formed. The morphogenesis of the skeletal elements is achieved by the interaction of the apical ectodermal ridge at the distal margin of the limb bud and the mesoderm. This was first shown by Saunders (1948) and the literature was reviewed, among others by Zwilling (1961) and Faber (1971). By six to nine days, the limb paddle elongates. The phalanges appear first as precartilaginous condensations and later as embryonic cartilage. The contour of the digits are sculptured in the way that the tissues between the digits are resorbed by processes

implying massive cell deaths (Glücksman 1951, Saunders et al. 1962).

At seven days, the mesenchymal cells of the foot plate are densely packed beneath the ectoderm. At eight to nine days, these mesenchymal cells differentiate into tendons, tendon sheaths, joint capsules, and subepidermal mesenchyme. The separation of tendons and tendon sheaths from subepidermal mesenchyme starts in the proximal part of the foot plate (Plate IA) and proceeds distally. By nine days of incubation, this process is completed in all parts of the digit (Plate IB). The surface of the digit is smooth (Fig. 6).

The following description concerns the development of pad III:1, pad III:2, and pad III:2/3, and the furrows that border or subdivide these pads.

Nine days

At nine days of incubation, the plantar surface of digit III is smooth (Fig. 6; Plate IB). The epidermis consists of one layer of cubical to cylindrical basal cells, measuring 8-10 μm , and one layer of flattened peridermal cells. The total thickness of the epidermis is 10-12 μm .

Beneath the epidermis, the subepidermal mesenchyme is not differentiated into dermis and subcutis, but the superficial mesenchymal cells are more closely packed than the deep lying cells. They form a dense dermal layer 15-20 μm thick. The dense dermal layer has 3.2 nuclei/1,000 μm^3 , and the subepidermal mesenchyme 2.4 nuclei/1,000 μm^3 (six individuals). The deep mesenchymal cells are more loosely arranged compared with earlier stages.

Ten days

At ten days of incubation, pad III:1 and pad III:2/3 have developed to the stage of pad bud, and the skin that borders these pads to the stage of furrow rudiment (Fig. 6; Plate IIA, IIB, IIIA, IIIB). Pad III:2 has not proliferated and consequently not reached the stage of pad bud (Fig. 6).

In the middle of pad III:1 and pad III:2/3, the basal cells have elongated and measure 10-12 μm , the total epidermis being 12-15 μm . The dense dermal layer has increased to 25-30 μm in the middle of the pads, but is still 15-20 μm in the lateral parts. The density in dense dermis in the middle of the pads has increased to 3.5 nuclei/1,000 μm^3 (ten individuals, $P < 0.05$).

The thickness of epidermis and dense dermis in pad III:2 is unchanged compared with the condition at nine days of incubation.

The furrows that delimit pad III:1 and pad III:2/3 have developed to the stage of furrow rudiment (Plate IIA, B, IIIA). The basal cells in the furrow are 14-18 μm , and the total epidermal thickness is 20-24 μm . The periderm has one thin superficial layer and one thick deep layer.

The basal cells in the early furrow rudiment are high and cylindrical with

elongated nuclei oriented perpendicularly to the surface. In a somewhat more advanced stage, the basal cells become wedge-shaped with the point towards the surface. Certain cells may round off and their nuclei assume a spherical shape (Plate IC). These changes are the first morphological signs of the formation of the hinge.

The hinging of the furrow is accompanied by a bulging of the adjacent pad (Fig. 6). This bulging is produced in part by an increased number of subepidermal cells. This was verified in the colchicine treated embryos (Plate IVA). Seven hours of colchicine treatment (one embryo) arrested 14 per cent of the nuclei in the subepidermal mesenchyme compared with three per cent in the dense dermis and seven per cent in the basal epidermal cells. During the proliferation, the mesenchymal cells become more dispersed (Plate IIA, IIB). The density in subepidermal mesenchyme varied from 1.7 to 2.4 nuclei/1,000 μm^3 (seven individuals examined); therefore the bulging of the pad is in part produced by an increased amount of intercellular substance.

Eleven days

At eleven days of incubation, pad III:1 and pad III:2/3 have developed to pad stage. They are delimited by furrows in furrow stage (Fig. 6; Plate IIC). The skin in pad III:2 has not proliferated, and the surface is almost flat between the two other pads.

The epidermis in pad III:2/3 is without any signs of further differentiation compared with the condition at ten days of incubation. The basal cells are still 12-15 μm , and the total epidermal thickness is 16-20 μm . The periderm is two-layered. The skin in the middle of pad III:1 has differentiated to the stage of papilla rudiment (see below).

The subepidermal mesenchyme of pad III:1 and pad III:2/3 has differentiated into dermis and subcutis, the latter with more spacious arrangement of cells (Plate IIIC). The border between the two tissues is distinct. The subcutis has 1.5 nuclei/1,000 μm^3 and dermis 2.4 nuclei/1,000 μm^3 . Many of the subcutaneous cells are oriented perpendicularly to the pad surface and focused towards the joint capsule, which indicates the direction of bundles of collagenous fibres that will later develop and anchor the skeletal elements to the dermis (Plate IID). Pad III:2 also shows a differentiation of subepidermal cells into dermis and subcutis, but the subcutis is thin (Fig. 6).

At eleven days of incubation, the furrows delimiting pad III:1 and pad III:2/3 penetrate deep into the plantar surface of the foot (Plate IIC). This is brought about by proliferation of epidermal cells in the furrow. During seven hours of colchicine treatment (three specimens), 7-12 per cent of the epidermal cells in the furrow are arrested compared with 1-3 per cent in the middle of the pad.

Pad III:2 is subdivided by one or two furrows and the development of these furrows shows an individual variation in number and localization (Fig. 3). The development of these furrows also starts with thickening of the basal cells; thus they develop in the same way as the furrows at pad III:2/3, but the number of thickened basal cells is less.

Twelve days

By twelve days of incubation, the furrows that subdivide pad III:2 have developed to the furrow stage (Fig. 6), and there is no morphological difference between these furrows and those developed earlier at pad III:1 and pad III:2/3.

The subcutaneous tissue in pad III:1 and pad III:2/3 is further dispersed, the density being 1.0-1.3 nuclei/1,000 μm^3 .

Times for development of furrows

The furrows do not develop at the same time in the different parts of the plantar skin. The time for the skin in the four digits to reach the furrow stage is shown in the diagram in Fig. 7. The following statements also concern the development to the early furrow stage.

At ten days, there are longitudinal furrows at phalanx III:4, but no other furrows have developed.

At eleven days, a great many furrows have developed. The four pads, number 1, are demarcated from the claws by furrows.

At twelve days, pad II:2 and pad III:2 are subdivided by furrows. The furrow that subdivides proximal pad II:3 and the furrow that demarcates the distal pad III:4 from the central pad have developed.

At twelve days, the furrow that separates pad IV:2/3 from pad IV:3 has developed in certain birds. The furrow that separated pad IV:3/4 and pad IV:4 develops at the same time. It is noteworthy that these furrows proximal to the joint pads develop about one day later than the distal furrow at the same pads. Usually, as for instance in pad III:2/3 (Fig. 6, 7), the distal and the proximal furrow at a pad develop at the same time. The time displacement is obviously related to the individual variation: the furrow may either develop comparatively late or may fail to develop.

Pad III:4 is subjected to individual variation (Fig. 3). At eleven days, the bud of the distal pad III:4 has developed and is demarcated from pad III:3/4 by a furrow. The furrow at the proximal side of the distal pad III:4 develops after one further day of incubation, at twelve days. Most specimens have the central pad extending to the proximal half of phalanx III:4. The latter pad is then regarded as a fusion of the central pad and a pad at middle and proximal half of phalanx

III:4. A minority of chicks have one or two pads at the proximal half of phalanx III:4 (not shown in Fig. 7). The furrows that demarcate these pads develop later than thirteen days of incubation; the time for their appearance could not be established in the examined material.

Development of papilla

By eleven days of incubation, the skin in the middle of pad III:1 has a dense dermis with 3.7 nuclei/1,000 μm^3 . In the dense dermis, the cells aggregate to dermal condensations with 4.0 nuclei/1,000 μm^3 (ten papillae, three individuals). The adjacent epidermis forms an epidermal placode, where the basal cells are 18-21 μm and the total thickness is 22-25 μm . The skin has then developed to a papilla rudiment (Plate IIID, IVB).

The papilla rudiment in the middle of pad III:2/3 develops a little later than those in pad III:1. The dense dermis has 3.9 nuclei/1,000 μm^3 , and the dermal condensation has 4.2 nuclei/1,000 μm^3 (eighteen papillae, six individuals). These values are significantly separated from those in pad III:1 ($P < 0.01$).

The papilla rudiments have dermal condensations that are 80-100 μm in diameter. The rudiments in pad III:2/3 lie closer together than those in pad III:1.

The nuclei in the condensed cells in the papilla rudiment differ from the adjacent cells in being slightly larger and more rounded (Plate IVC). They seem to occupy a large part of the cell volume. The nuclei of the basal cells in the epidermal placode move towards the periphery, leaving a nuclei-free zone next to the dermis. These changes are obviously the morphological signs of a differentiation process. Similar localization of epidermal nuclei and enlargement of dermal cells have been observed in the scale rudiment (Yohro 1969) and feather rudiment (Wessels 1965), and it has been correlated with a non-mitotic phase of development (Wessels 1965).

During the further development the epidermis bulges out and the dermoepidermal junction follows (Plate IVD). The skin has then developed to the stage of a papilla bud. In the middle of the papilla, the thickness of epidermis is unchanged; basal cells are 15-18 μm and total epidermis is 19-22 μm . In the margins of the papilla, the basal cells are higher, 18-21 μm , and the total thickness is 22-25 μm . There are rounded dermal cells both in the middle of the papilla and at the turned in margin. Mitoses were observed both in epidermis and dermis, in the middle and also in the margin of papilla. This suggests that there is a proliferation and differentiation both at the middle and at the margin of the papilla during the stage of the papilla bud.

The first papillae develop in the centre of the pad, and new papillae appear peripherally to the one first established. Thus the skin in the middle of the pad

may be in the stage of papilla bud, whereas the adjacent skin is in the stage of papilla rudiment. About two days after the development of the first papillae, the whole surface of the pad is covered with papillae (Plate IID).

The outward growth of the papilla continues, and the epidermal surface of the papilla margin turns inward so that the surface, as seen in section, forms an acute angle. The skin has then differentiated to the stage of early papilla. This stage was not further examined in the present study.

Times for development of papillae

The papillae develop to the stage of papilla bud at different times in the different pads, as shown in the diagram in Fig. 8. At eleven days of incubation, the papillae develop in the three distal pads of the anterior digits, pad II:1, pad III:1, pad IV:1, and also in the central pad. After a further day of incubation, at twelve days, the six joint pads in the anterior digits have got papillae. At thirteen days, only two new pads have got papillae, distal pad II:3 and pad I:1. At fourteen days, the remaining pads, which are phalanx pads, have got papillae. The skin between the central pad and the distal pad III:4 differentiates to papilla bud later than fourteen days (cf. "Development of furrows and pads"); however, the time for this differentiation could not be stated in the examined material.

DISCUSSION

The most rapid development of the digits occurs during the first nine days of incubation. Thereafter the growth rate is reduced (Fig. K; measurements on digit length by Hamburger & Hamilton, 1951). It is after this phase of rapid length growth of the leg that the differentiation of the plantar skin into furrows, pads, and papillae takes place.

In the early limb bud, the subepidermal space is filled with densely packed mesenchymal cells. First, skeletal elements are differentiated; then tendons, tendon sheaths, and joint capsules. When this development is completed after **about** nine days of incubation, the subepidermal mesenchyme is restricted to a layer between the epidermis and the skeletal elements. It is organized into one superficial layer of dense dermis and one deep layer of more loosely arranged cells. Morphologically, this stage of development is comparable to the first stage in the development of the skin in the feather-forming areas. By five to six days of incubation, the mesenchymal cells accumulate to a 40 μ m thick layer below the epidermis in the dorsal region of the spinal feather tract (Wessels 1965, Sengel 1971). A similar dense layer develops by eight to nine days on the frontal part of the shank, where the large scales will later develop (Sawyer 1972 a). By ten

days of incubation, the dense dermal layer is 15-20 μm in the plantar surface; by eleven days, it has increased to 20-25 μm in the middle of the pad buds, where the first papillae will appear.

The nuclear density in dense dermis of pad III:1 and pad III:2/3 by nine days of incubation, before the development of the papillae, is 3.2 nuclei/1,000 μm^3 , and increases to 3.5 nuclei/1,000 μm^3 by ten days of incubation. By eleven days, the dense dermis has 3.7 nuclei/1,000 μm^3 and the dermal condensation in papilla rudiment 4.0 nuclei/1,000 μm^3 in pad III:1. The corresponding values for pad III:2/3 are 3.9 and 4.2 nuclei/1,000 μm^3 . The dense dermis in the spinal feather-forming area by five to six days is 2.8 nuclei/1,000 μm^3 but increases to 5.5 nuclei/1,000 μm^3 in the dermal condensation of feather rudiment (Wessels 1965). The density in scale rudiment by ten days of incubation, the asymmetrical placode stage of Sawyer, is 3.2 nuclei/1,000 μm^3 . These density values indicate that the dense dermis in the plantar surface by ten days of incubation before the development of the papilla rudiment is denser than the corresponding layer in the spinal feather-forming area before the development of feather rudiment and is comparable to that in the scale rudiment by the same time of development. The development of skin structures implies an increased density in dense dermal layers, and the appearance of dermal condensations occurs at different times in that general trend. The difference in cell density between the dermal condensation of one papilla rudiment and adjacent dense dermis is much less than the difference between dermal condensation in the feather rudiment and dense dermis in the feather-forming area.

The first morphological signs of the furrow is an increased height of basal epidermal cells. Then the cells in the middle of the furrow rudiment change shape from columnar to wedge-shaped and later rounded, which results in the hinging of the rudiment.

The furrow rudiment has not previously been described and the mechanism of the epidermal thickening and the hinging process is unknown. Many furrows develop in every individual and in the same site of the plantar skin (Fig. E, C). The size of the pads is a characteristic of different species (p. 39). This indicates that the furrows develop by morphogenetic processes depending on genetic factors.

The furrows that subdivide pad II:2, pad III:2, and pad III:4 develop at different sites in respective pad, and their localization might be an effect of the bending of the digit. But the development from the furrow rudiment to furrow stage is similar to the development of the other furrows, and if mechanical factors are involved, they might be restricted to the phase of induction and early development.

The furrow between pad IV:2/3 and pad IV:3 develop in certain individuals, but fail to develop in others. Similar circumstances are valid for the furrow between pad IV:3/4 and pad IV:4. This individual variation does not occur in the pheasant,

where both furrows always develop. The variation in the hen might be a feature of the species or a feature of the studied race.

No substantially raised mitotic activity in the furrow rudiment could be observed, either in the normal preparations or in those successfully treated with colchicine. Even if the mechanism involves a higher mitotic activity, this would not inevitably lead to a folding of the tissue. Morphogenetic movements of large groups of cells in which curved structures are formed from flat sheaths are known to occur frequently in animal development (Trinkaus 1965). Microfilaments have been shown to occur in such cells, i.e. the lense placode (Wrenn & Wessels 1969), and the evidence from this and other organs supports the conclusion that these microfilaments constitute a contractile mechanism that is responsible for the morphogenetic movement (Wessels et. al. 1971). The changed shape of basal cells might tentatively be caused by similar morphogenetic events.

The morphological development of the papilla is similar to that of the feather (Wessels 1965, Sengel 1971) and the scale (Sawyer 1972a) concerning the information of a dermal condensation and an epidermal placode, but the scale rudiment is smaller. The dermal condensation in the scale rudiment is 80-100 μm compared with 235 μm in the feather rudiment (Wessels 1965, Wessels & Evans 1968). The epidermal placode in the feather and scale rudiments has basal cells that slant towards the centre of the placode, which is not the case in the papilla placode. Recombination experiments with papillae have shown that dermis controls both the structure and spatial arrangement of papilla development (Linsenmeyer 1972); these results are in conformity with those on feather development (Sengel 1971).

The morphogenetic movements of the papilla are similar to those in the feather (Wessels 1965). In both, the centre of the rudiment bulges out. In the scale of the frontal shank, the rudiment undergoes an off-centring process so that the distal part of the scale becomes the top and the dermal condensation underlies it (Sayer 1972a). The development of the minor scales in the sides of the digit has not been so carefully studied. The off-centring process does not seem to occur and the development is more similar to that of a papilla.

The first papillae to appear are those in central pad and pad II:1, pad III:1, and pad IV:1. After one more day of incubation, the papillae in the joint pads develop; and after yet another day, those in the phalanx pads. This sequence of development seems to be correlated with the function. The flexor muscles insert by the principle tendon branch on the bases of phalanges lying dorsal to the joint pads. When the muscles contract, these pads press against the substrate. The joint pads are probably subjected to heavier wear against the substrate than are the phalanx pads.

LITERATURE

- Cohen, J. 1966. Feathers and patterns. Pp. 1-38 in Abercrombie, M & Brachet, J. (eds.): *Advances in Morphogenesis*. Academic Press, New York & London.
- Cohen, J. 1969. Dermis, epidermis and dermal papillae interacting. Pp. 1-18 in Montagna, W. & Dobson, R.L. (eds.): *Advances in Biology of Skin*, Vol. IX. Hair Growth. Pergamon Press, Oxford.
- Faber, J. 1971. Vertebrate limb ontogeny and limb regeneration: morphogenetic parallels. Pp. 127-147 in Abercrombie, M., Brachet, J. & King, T.J. (eds.): *Advances in morphogenesis*, Vol. 9. Academic Press, New York & London.
- George, J.C. & Berger, A.J. 1966. *Avian Myology*. Academic Press, New York & London.
- Glücksman, A. 1951. Cell deaths in normal vertebrate ontogeny. - *Biol. Rev.* 26:59-86.
- Goetinck, P.F. & Sekellick, M.J. 1972. Observations on collagen synthesis, lattice formation, and morphology of scaleless and normal embryonic skin. - *Develop. Biol.* 28:636-648.
- Hamburger, V. & Hamilton, H.L. 1951. A series of normal stages in the development of the chick embryo. - *J. Morphol.* 88:49-92.
- Linsenmeyer, T.F. 1972. Control of integumentary patterns in the chick. - *Develop. Biol.* 27:244-271.
- Melander, Y. & Wingstrand, K.G. 1953. Gomori's hematoxylin as a chromosome stain. - *Stain Technol.* 28:217-223.
- Rawles, M. 1963. Tissue interactions in scale and feather development as studied in dermal epidermal recombinations. - *J. Embr. Exp. Morph.* 11:765-789.
- Saunders, J.W. 1948. The proximo-distal sequence of origin of the parts of the chick wing and the role of the ectoderm. - *J. Exp. Zool.* 108:363-403.
- Saunders, J.W., Jr., Gasseling, M.T. & Saunders, L.C. 1962. Cellular death in morphogenesis of the avian wing. - *Develop. Biol.* 5:147-178.
- Sawyer, R.H. 1972a. Avian scale development. I. Histogenesis and morphogenesis during formation of the scale ridge. - *J. Exp. Zool.* 181:365-384.
- Sawyer, R.H. 1972b. Avian scale development. II. A study of cell proliferation. - *J. Exp. Zool.* 181:385-408.
- Sengel, P. 1958. Recherches expérimentales sur la différenciation des germes plumeux et du pigment de la peau de l'embryon de Poulet en culture in vitro. - *Ann. Sci. Nat. Zool.* 20:431-514.
- Sengel, P. 1964. The determinism of the differentiation of the skin and the cutaneous appendages of the chick embryo. Pp. 15-34 in Montagna, W. & Lobitz, W.C. (eds.): *The Epidermis*. Academic Press, New York & London.
- Sengel, P. 1971. The organogenesis and arrangement of cutaneous appendages in birds. Pp. 181-230 in Abercrombie, M., Brachet, J. & King, T.J. (eds.): *Advances in morphogenesis*, Vol. 9. Academic Press, New York & London.
- Sengel, P. & Patou, M.P. 1969. Experimental conditions in which feather morphogenesis predominates over scale morphogenesis. - *Nature* 222:693-694.
- Stuart, E.S. & Moscana, A.A. 1967. Embryonic morphogenesis: role of fibrous lattice in the development of feathers and feather patterns. - *Science* 157:947-948.
- Thomson, J.L. 1964. Morphogenesis and histochemistry of scales in the chick. - *J. Morph.* 115:207-224.

- Trinkaus, J.P. 1965. Mechanisms of morphogenetic movements. Pp. 55-104 in DeHaan, R.L. & Ursprung, H. (eds.): Organogenesis. Holt, Rinehart & Winston, New York.
- Wessels, N.K. 1961. An analysis of chick epidermal differentiation in situ and in vivo in chemically defined media. - Develop. Biol. 3:355-389.
- Wessels, N.K. 1962. Tissue interaction during skin histodifferentiation. - Develop. Biol. 4:87-107.
- Wessels, N.K. 1965. Morphology and proliferation during early feather development. - Develop. Biol. 12:131-153.
- Wessels, N.K. & Evans, J. 1968. The ultrastructure of oriented cells and extracellular materials between developing feathers. - Develop. Biol. 18:42-59.
- Wessels, N.K., Spooner, B.S., Ash, J.F., Bradley, M.O., Luduena, M.A., Taylor, E.L., Wrenn, J.T., & Yamada, K.M. 1971. Microfilaments in cellular and developmental processes. - Science 171:135-143.
- Wren, J.T. & Wessels, N.K. 1969. An ultrastructural study of lens invagination in the mouse. - J. Exper. Zool. 171:359-367.
- Yohro, T. 1969. The mitotic pattern of the embryonic epidermis of chick during scale morphogenesis. - J. Embryol. Exper. Morph. 21:235-242.
- Zwilling, E. 1961. Limb morphogenesis. Pp. 301-330 in Abercrombie, M. & Brachet, J. (eds.): Advances in Morphogenesis. Vol. 1. Academic Press, New York.

Plate I. (A) Sagittal section through digit III at 8 days. Phalanx III:3 and phalanx III:4 appear as embryonic cartilage, whereas the distal phalanges are mesenchymal condensations, morphologically undifferentiated. The proximal portion of the tendon for flexor and extensor muscles are differentiated from subectodermal mesenchyme, whereas the distal portions are still undifferentiated.

(B) Sagittal section through digit III at 9 days. The four phalanges appear as embryonic cartilage. The tendon of insertion for flexor muscles are differentiated from subectodermal mesenchyme. The superficial dense dermis and epidermis are heavily stained.

(C) Sagittal section through the furrow between pad III:2/3 (to the right) and pad III:2 at 10 days. Epidermis has differentiated to the stage of furrow rudiment, and the furrow has started to turn inward. The basal cells in the middle of the rudiment have rounded off.

Abbreviations: bc, basal cells; dd, dense dermis; pe, periderm; sm subepidermal mesenchyme; ph III:1, phalanx III:1; ph III:2, phalanx III:2; ph III:3, phalanx III:3; ph III:4, phalanx III:4; fldl, tendon of insertion for M. flexor digitorum longus; fppIII, tendon of insertion for M. flexor perforans et perforatus digiti III; edl, tendon of insertion for M. extensor digitorum longus. (A) and (B) are stained with Ehrlich's haematoxylin; (C), with Gomori's haematoxylin.

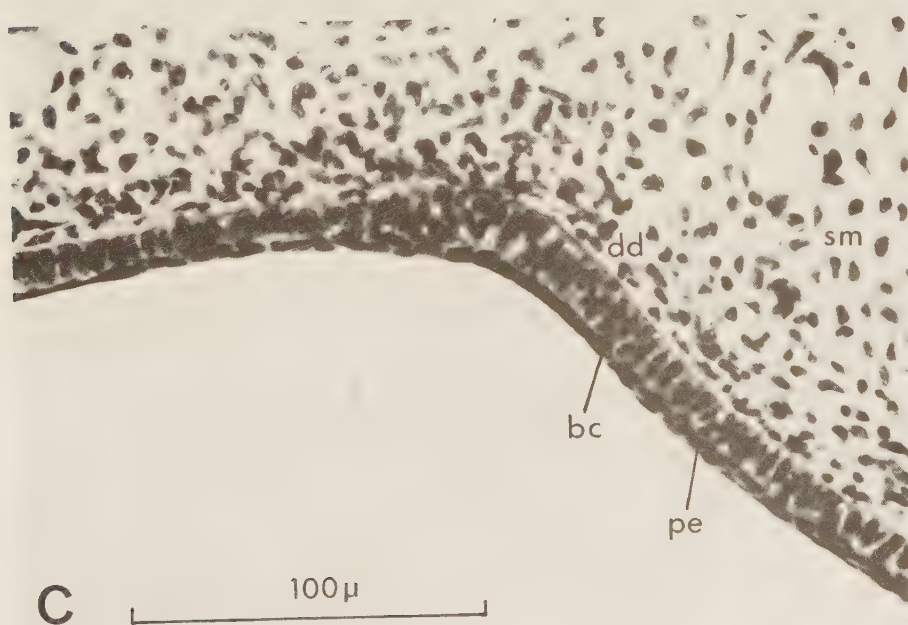
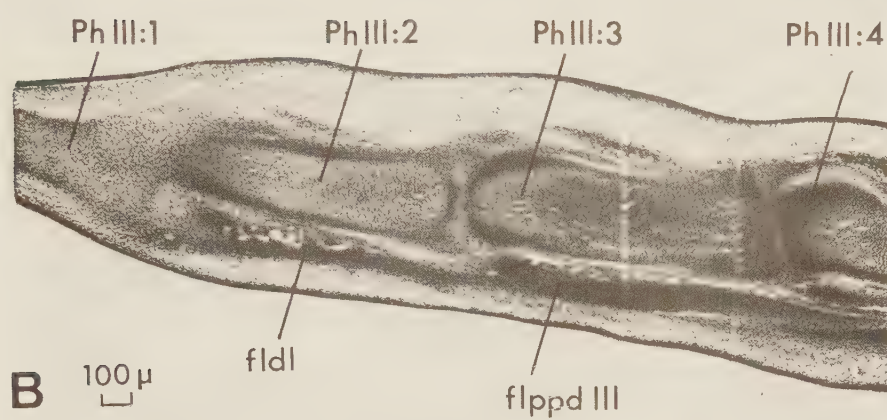
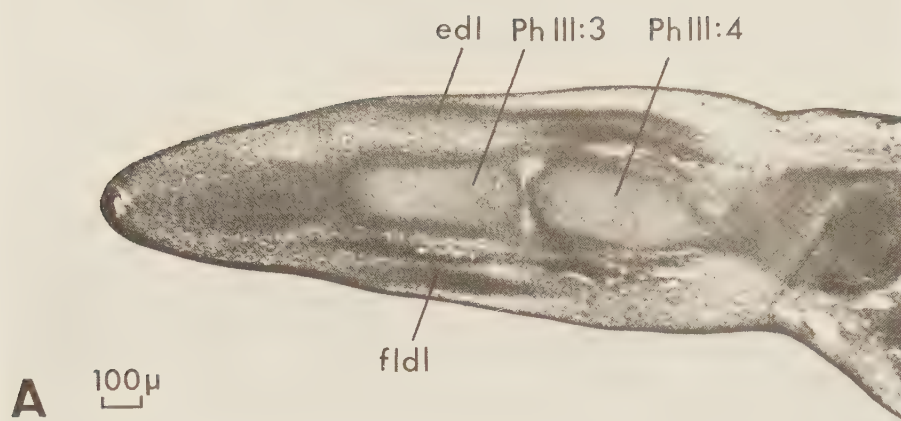


Plate II. Sagittal sections through pad III:2/3, (A) and (B) at 10 days, (C) at 11 days, (D) at 13 days.

(A) and (B) Embryos are the same age and the pads have developed to the stage of pad bud, but in (B) the furrows have begun to hinge inwards and the proliferation in subectodermal mesenchyme is somewhat more advanced than in (A).

(C) The pad has developed to the early pad stage, and the subectodermal mesenchyme is differentiated into dermis and subcutis.

(D) The papillae in the middle of the pad, the first to appear, have developed to the late part of papilla bud stage, whereas the papillae close to the furrows are in the early part of papilla bud stage.

Abbreviations: d, dermis; s, subcutis; sm, subectodermal mesenchyme; f, furrow; fdl, tendon of insertion for M. flexor digitorum longus; fppIII, tendon of insertion for M. flexor perforans et perforatus digiti III. (A), (B), and (C) are stained with Gomori's haematoxylin; (D), with Ehrlich's haematoxylin.

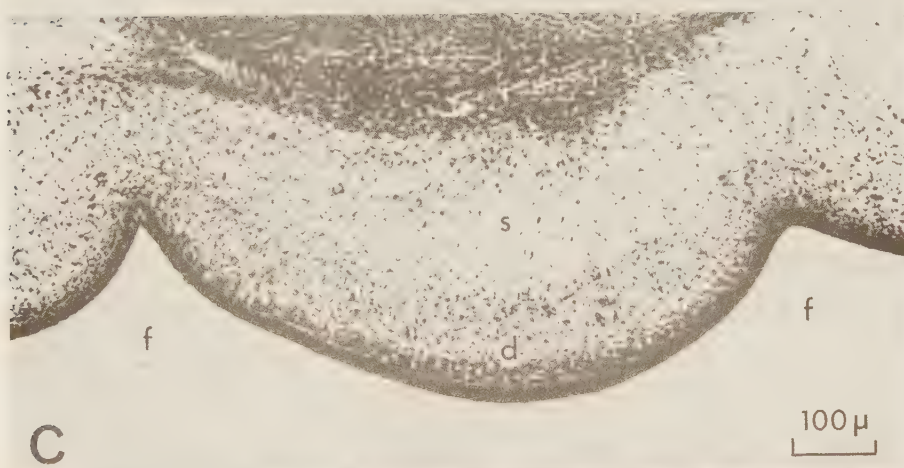
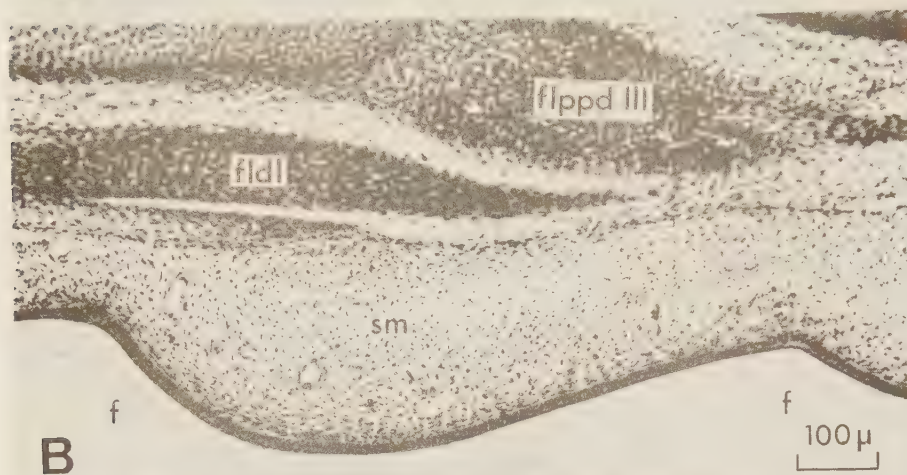
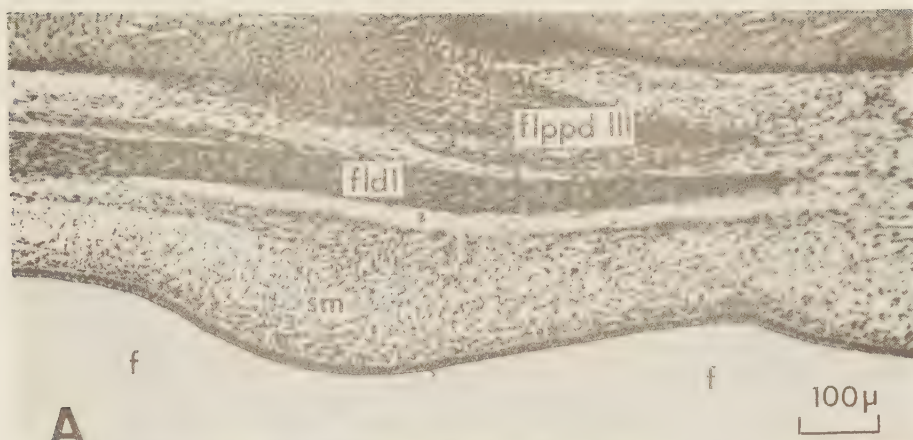


Plate III. (A) Transversal section through digit III at head of phalanx III:3 by 10 days. The furrow between pad III:2/3 and pad III:3 is in the stage of furrow rudiment.

(B) Transversal section through digit III at joint III:2/3 by 10 days in the same embryo as in (A) but distal to that section. Pad III:2/3 has developed to the stage of pad bud. The subectodermal mesenchyme is proliferating.

(C) Transversal section through digit III at head of phalanx III:2 at 11 days. Pad III:1 has developed to the stage of pad bud. Two papillae have developed to the stage of papilla rudiment.

Abbreviations: d, dermis; dd, dense dermis; f, furrow; jc, joint capsule; sm, subepidermal mesenchyme; s, subcutis; ph III:2, phalanx III:2, ph III:3, phalanx III:3; p, papilla. All sections are stained with Gomori's haematoxylin.

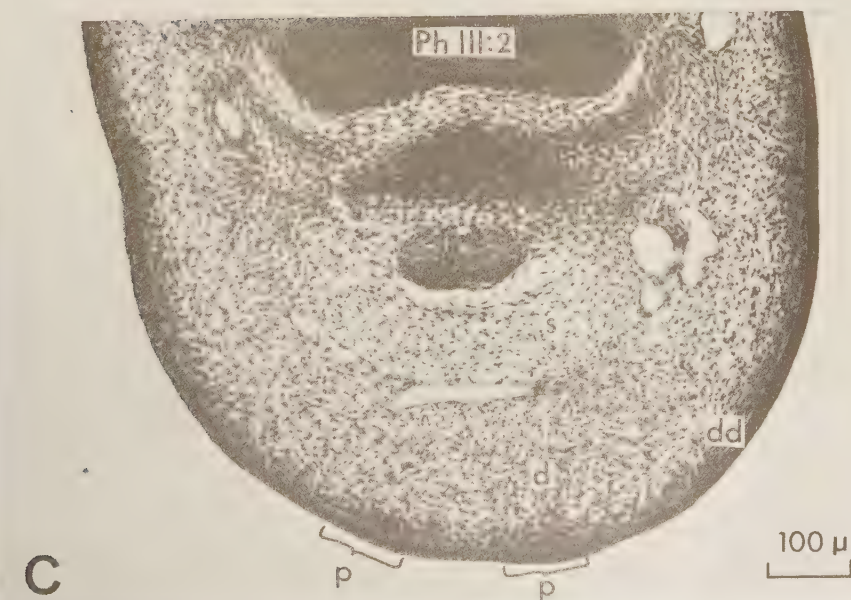
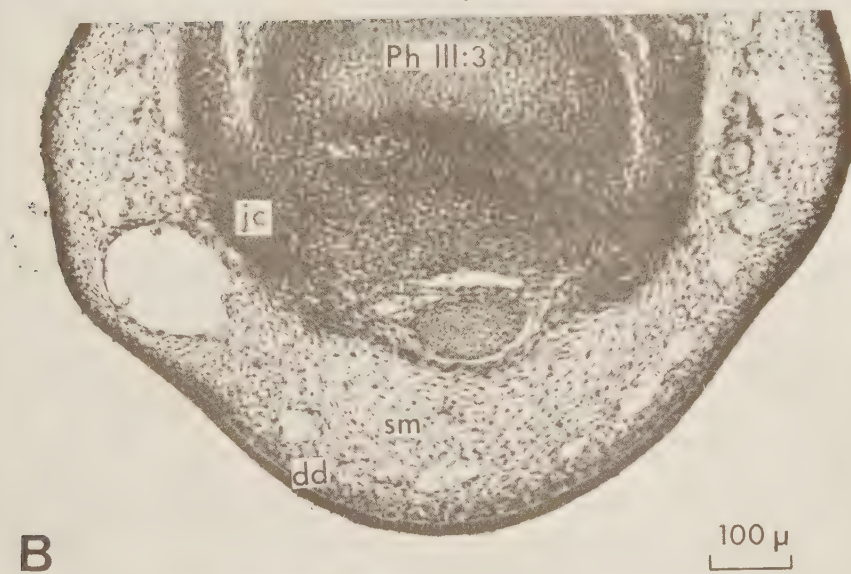
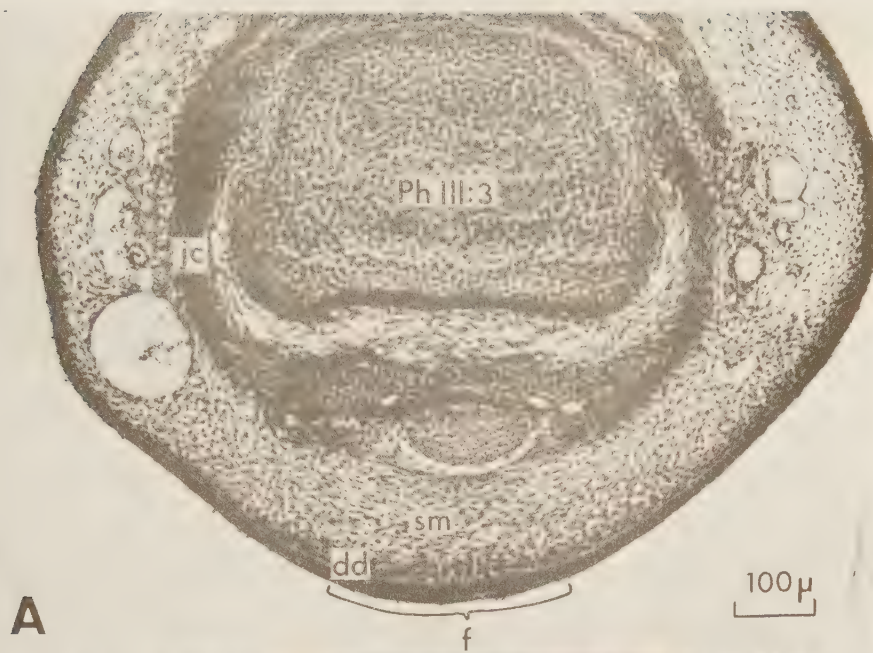


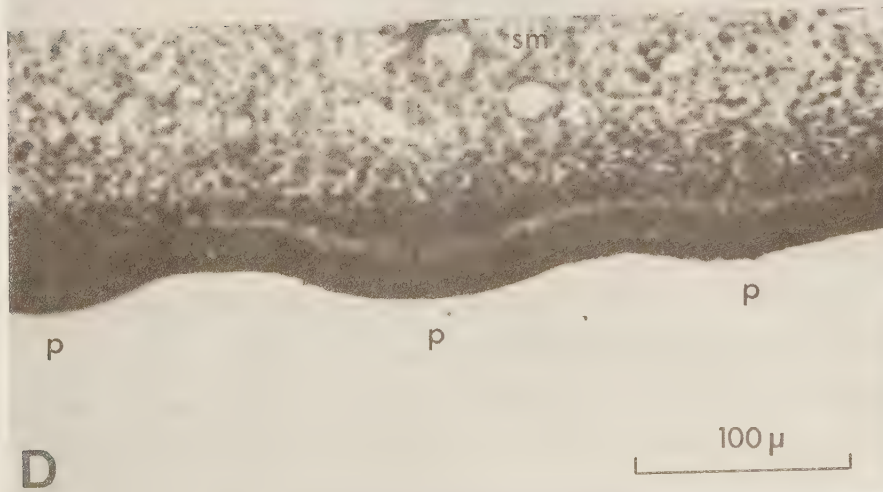
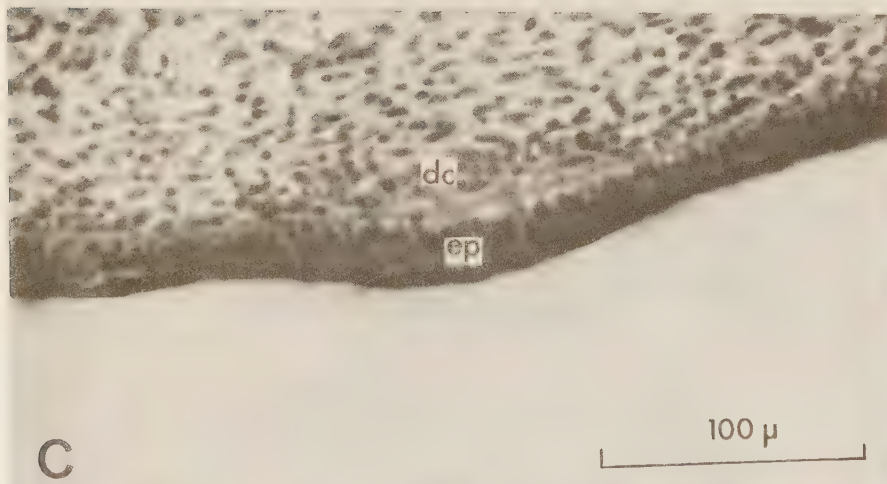
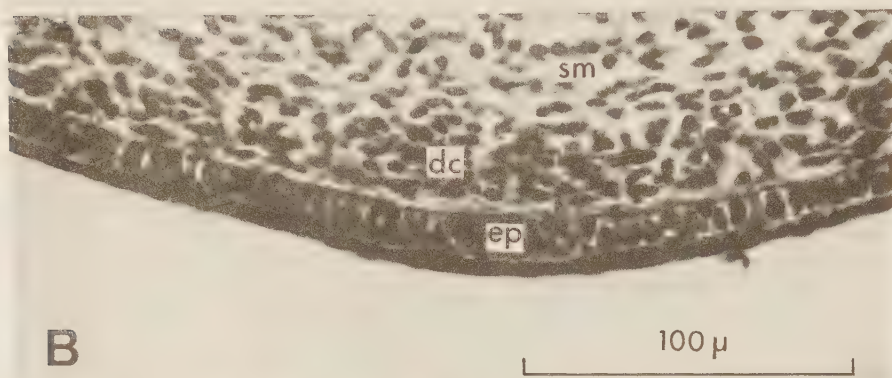
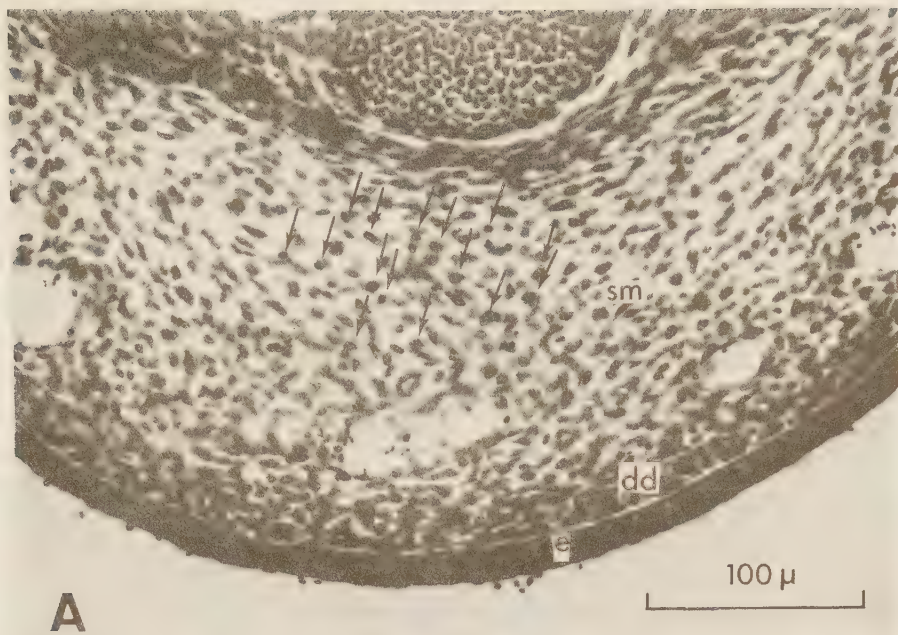
Plate IV. (A) Transversal section of digit III through pad III:2/3 at 10 days. The subectordermal mesenchyme is proliferating as indicated by the great number of mitoses (arrows), arrested by colchicine treatment for seven hours.

(B) Transversal section through pad III:1 at 11 days; detail of Plate III:C. The papilla in stage of papilla rudiment consists of a dermal condensation and an epidermal placode.

(C) Transversal section through pad III:1 at 11 days. The papilla rudiment is more advanced than in (B). The nuclei in the basal cells of the epidermal placode have aggregated in the superficial part of the cells, leaving a nuclei-free zone at the dermo-epidermal junction. The cells in the dermal condensation have enlarged nuclei. The surface of the papilla has protruded slightly but the dermi-epidermal junction is straight.

(D) Sagittal section through central pad by 12 days. The middle of the three papillae has developed to the stage of papilla bud, whereas the peripheral papilla to the right is in the stage of papilla rudiment.

Abbreviations: bc, basal cell; dc, dermal condensation; dd, dense dermis; e, epidermis; ep, epidermal placode; fdl, tendon of M. flexor digitorum longus; sm, subectordermal mesenchyme. (A) and (B) are stained with Gomori's haematoxylin; (C) and (D), with Ehrlich's haematoxylin.



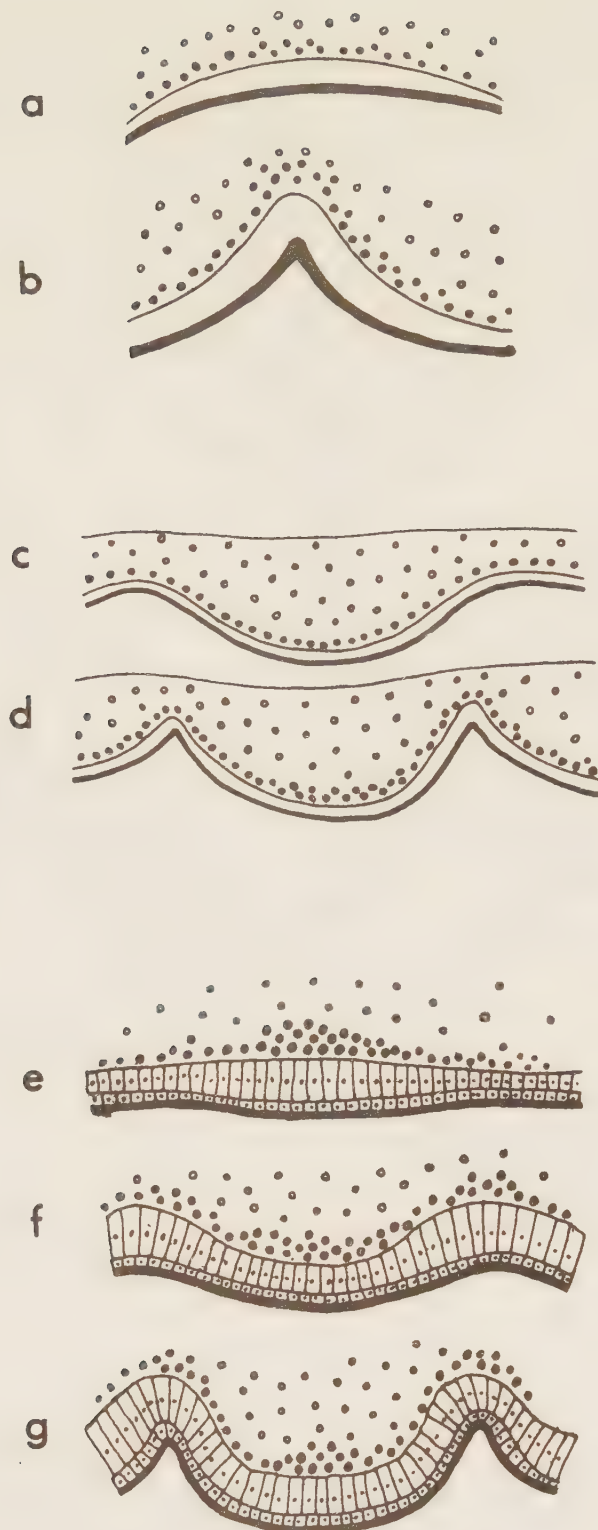


Fig. 1. Diagrams of developmental stages: (a) furrow rudiment, (b) early furrow stage, (c) pad bud, (d) early pad stage, (e) papilla rudiment, (f) papilla bud, and (g) early papilla stage. The periderm layer is indicated black and the basal cell layer in (a), (b), (c), and (d) unshaded. The cells in the superficial dense dermal layer are indicated by dots and the other subepidermal cells by rings. A line in (c) and (d) shows the deep border of the subepidermal mesenchyme.

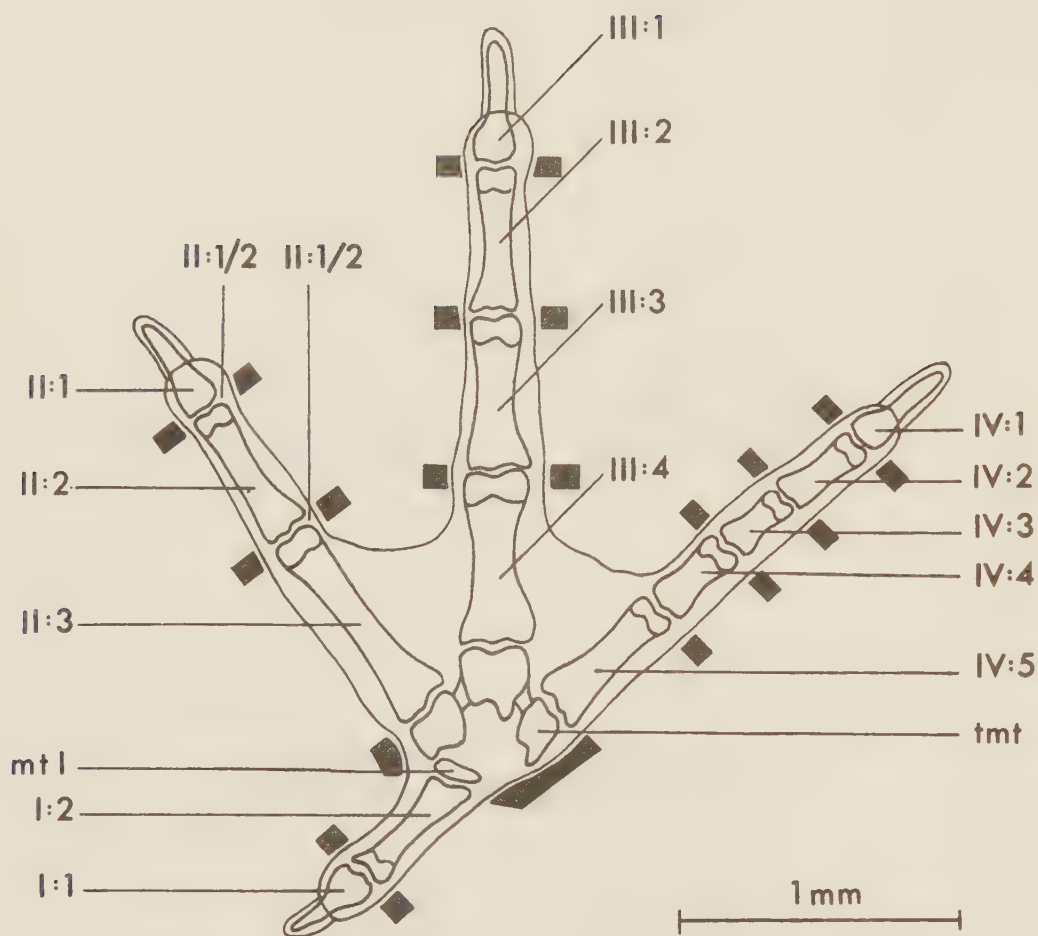


Fig. 2. Structure and designation of phalanges and joints. Digits are given Roman numerals and phalanges Arabic numerals. Joints are designated by the numerals of the participating phalanges, as shown by the joints in digit II. mt I, metatarsus I; tmt, tarsometatarsus. Black areas at the sides of the digits show the position of joints. Scale refers to length in one-day old chick.

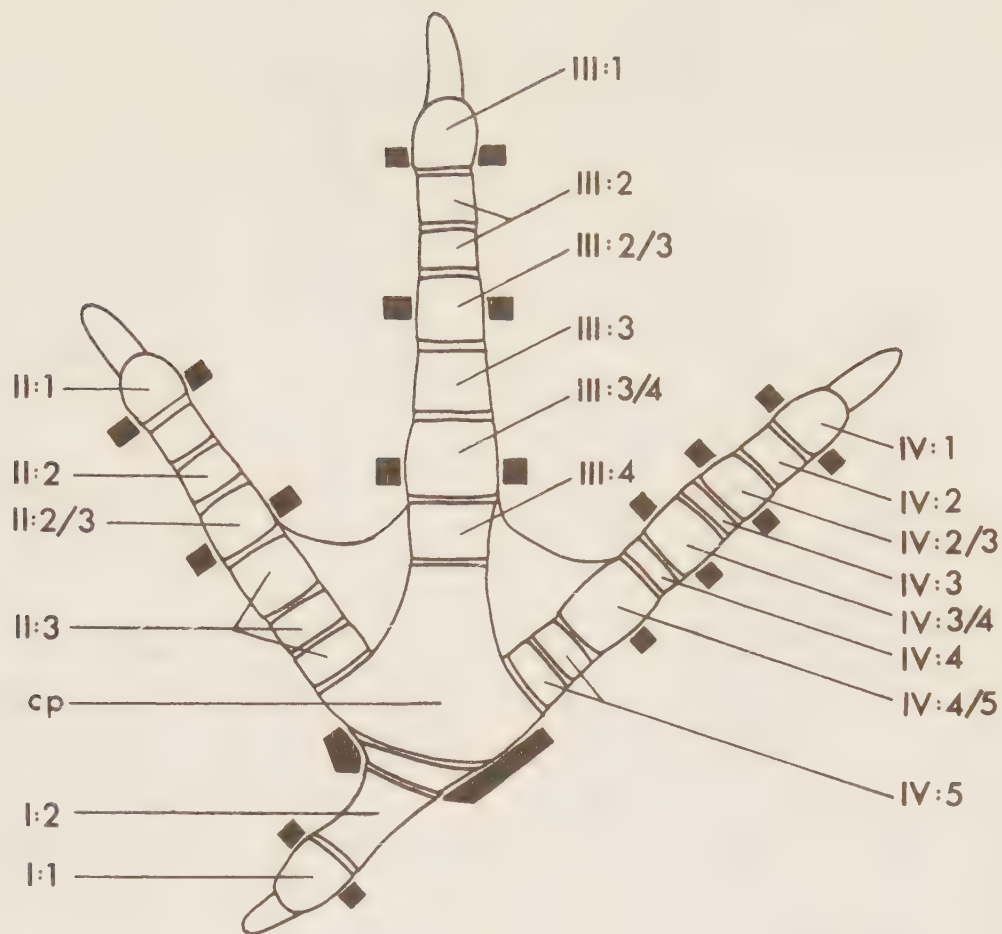
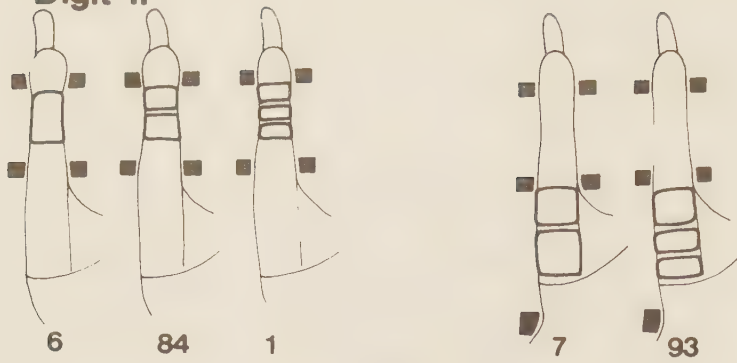
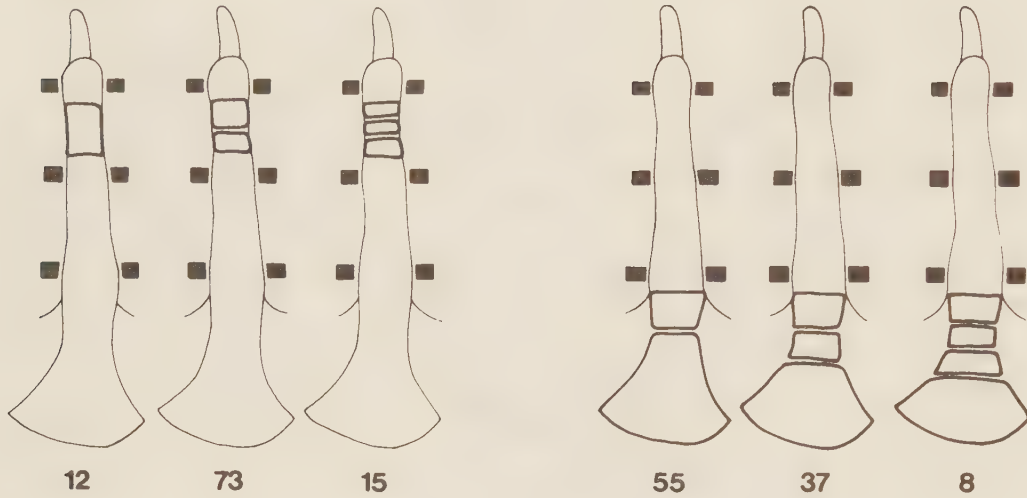


Fig. 3. Diagram of pads and furrows. Each pad is represented by a line, showing the margin of the pad. The designation of pads is made in accordance with the adjacent phalanx or joint. cp, central pad, lying ventral to the trochleas of tarsometatarsus. The black areas indicate the position of joints.

Digit II



Digit III



Digit IV

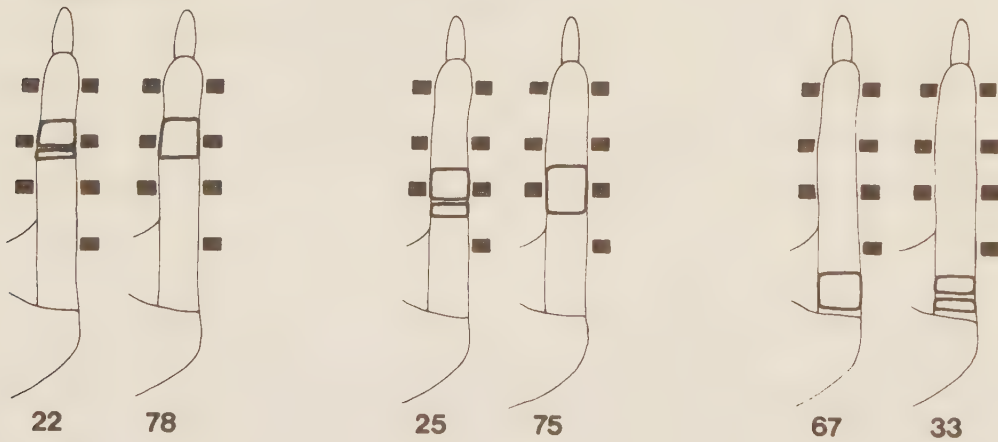


Fig. 4. Individual variation in pads and furrows. The plantar surface is divided into regions in which variation occurs. The types of pads in each region and the frequency in per cent of each type are shown. Black areas indicate the position of joints.

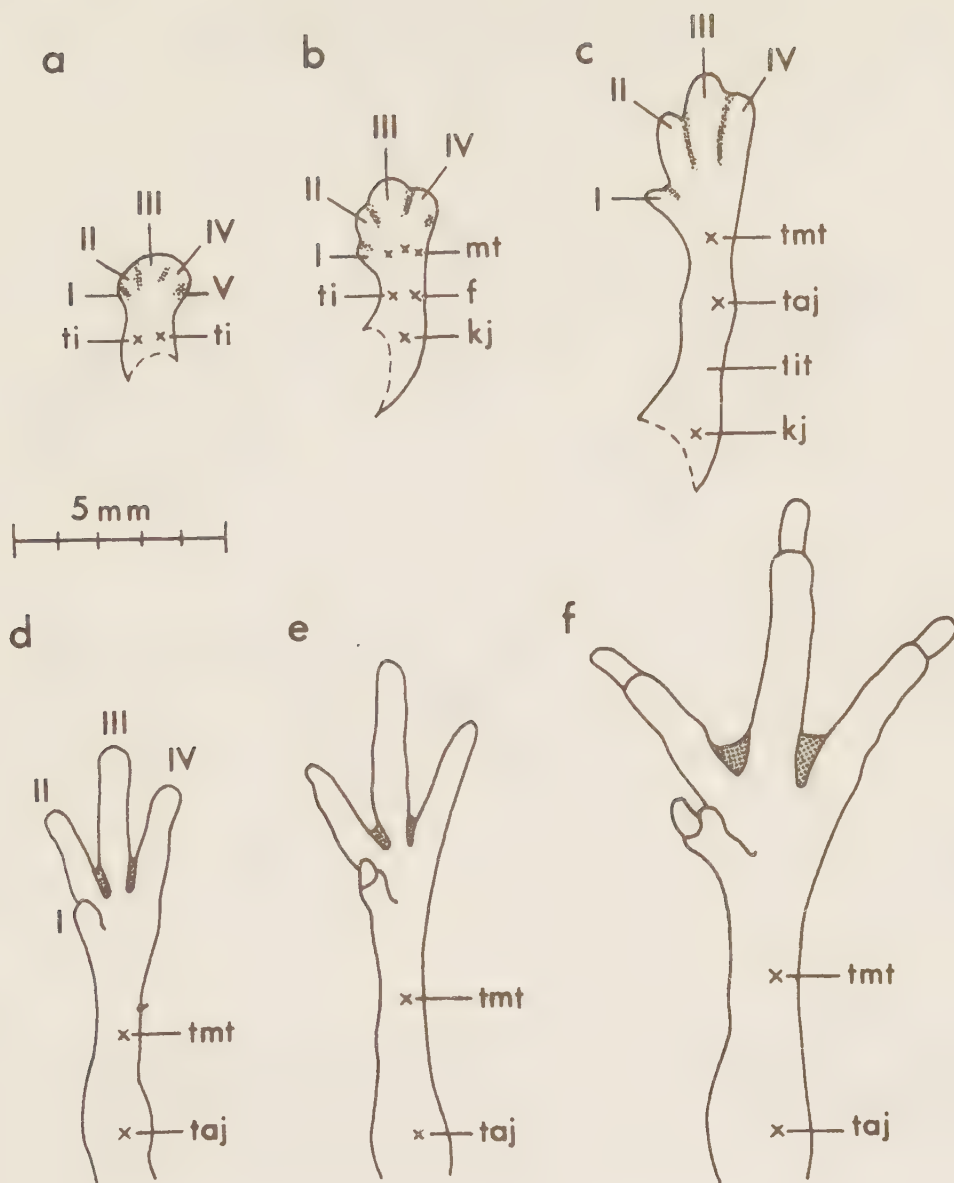


Fig. 5. Development of left hind leg at six through eleven days of incubation as seen in ventral view. The upper row shows the whole leg at (a) 6, (b) 7, and (c) 8 days of incubation; the lower row shows shank and foot at (d) 9, (e) 10, and (f) 12 days. At 12 days, most of furrows and pads have developed but they are not shown in the diagram. All diagrams are drawn in the same scale. Roman numeral indicates digit. The contour of skeletal elements are not shown but the position is indicated by crosses: ti, tibia; f, fibula; mt, metatarsals; tit, tibiotarsus; tmt, tarsometatarsus; kj, knee joint; taj, tarsal joint.

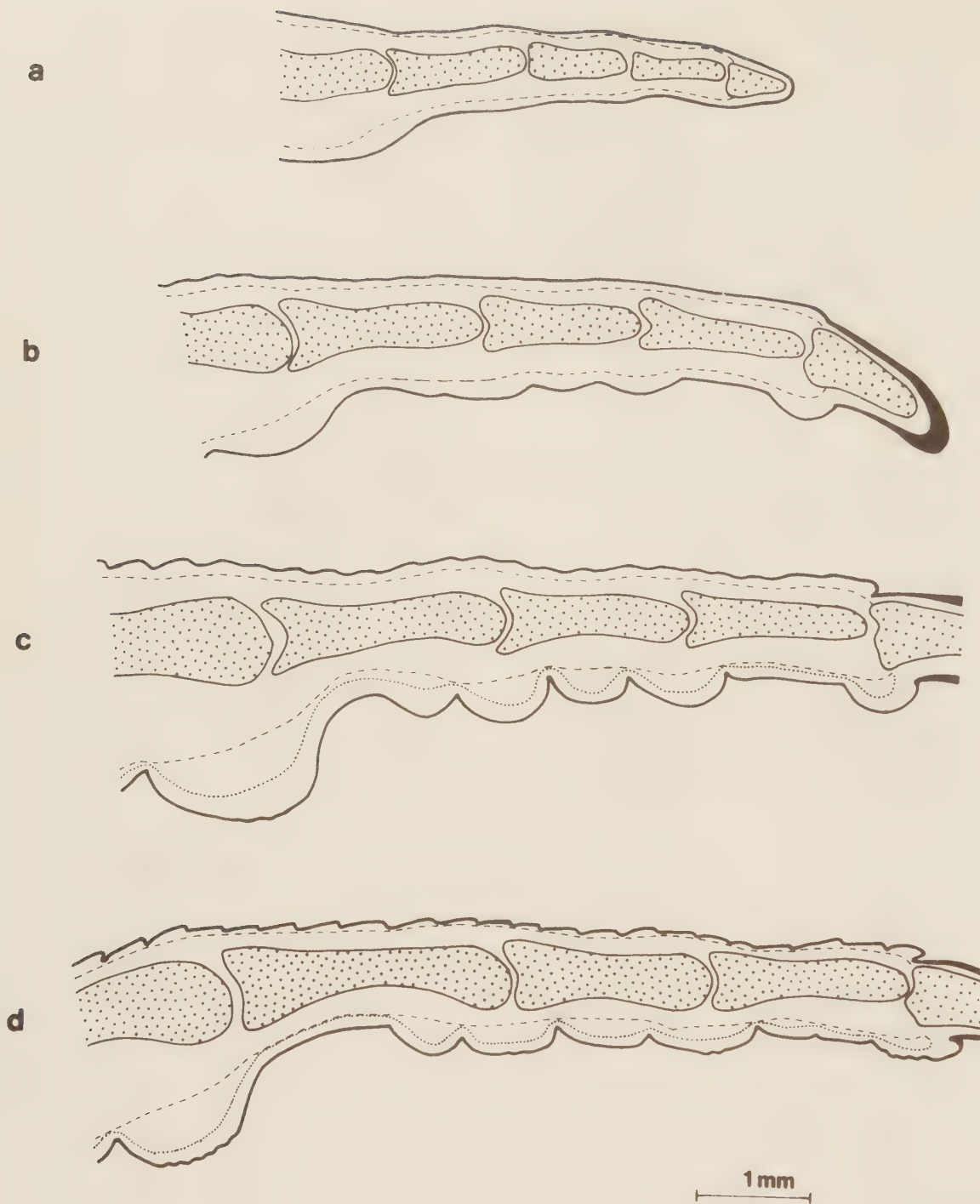


Fig. 6. Diagram of skin and skeletal elements in digit III: (a) at 9 days, (b) at 10 days, (c) at 11 days, and (d) at 12 days. Broken line shows deep border of undifferentiated mesenchyme or differentiated subcutis; spotted line shows border between dermis and subcutis. Epidermis is indicated black.

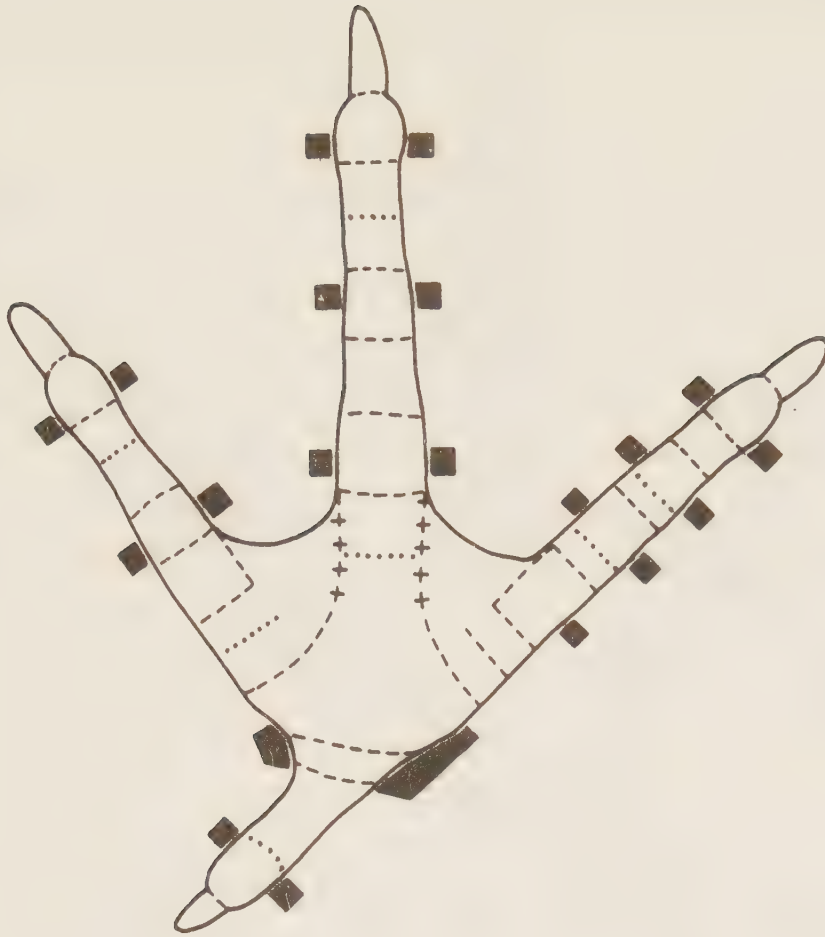


Fig. 7. Time for development of the different furrows to the early furrow stage. Crosses indicate furrows appearing at 10 days of incubation; broken lines, at 11 days; points, at 12 days. Black areas show the position of joints.

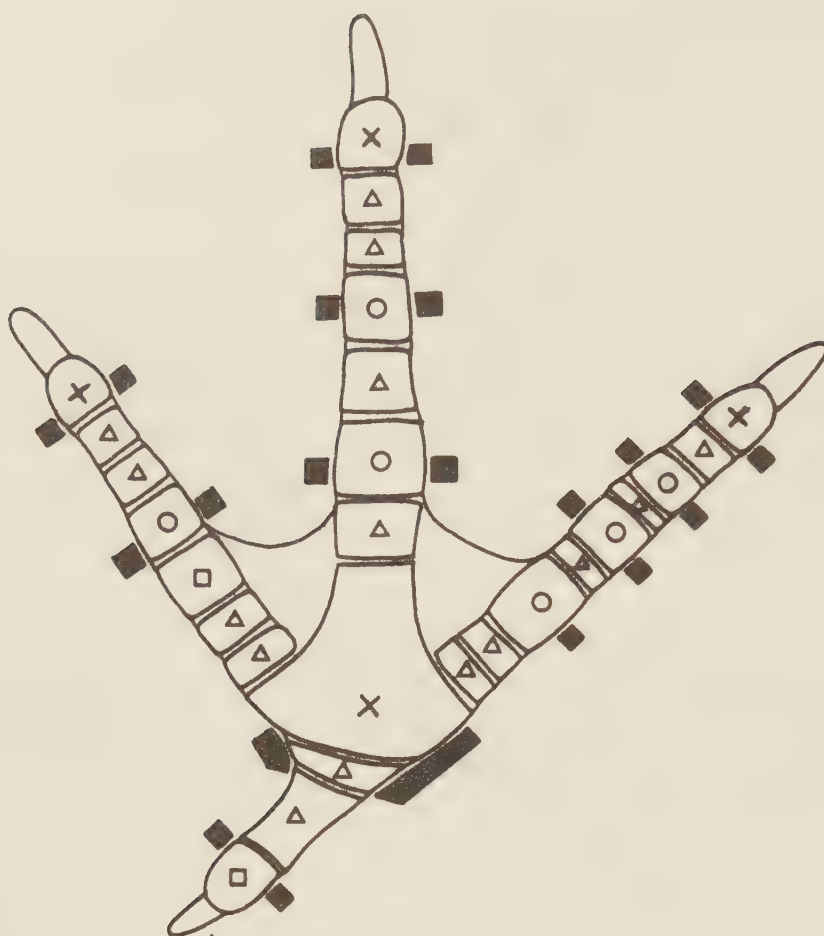


Fig. 8. Time for development of the first papillae in the different pads to the stage of early papilla bud. Cross indicates papillae appearing at 11 days of incubation; circle at 12 days; square, at 13 days; triangle, at 14 days.

III. Pattern of pads and folds in European passerine species.

ABSTRACT

A comparative study of pads and folds in the foot is made on 57 passerine species, classified in 18 families or subfamilies of the suborder Oscines.

A basic pattern of thirteen pads is recognized: twelve in the digit, each related to one phalanx; the thirteenth in the central part of the foot, ventral to the trochleas of tarsometatarsus. Certain pads in the anterior digits are subdivided in species with long and narrow pads.

The number of folds varies, even in the same species, but a basic pattern is recognized. There is one fold at each joint. Except for the folds at the distal joint in the four digits, these folds are homologous with pads in certain non-Passeriformes. The folds at the proximal phalanx of the third and the fourth digit are interpreted as reduced pads. Some folds are separated parts of phalanx pads.

Most passerine birds have this basic pattern of pads and folds, which are clearly adapted to a life on branches or on twigs. Certain species, exemplified by Alauda arvensis, Plectrophenax nivalis, Certhia familiaris, and Regulus regulus, have different morphology of pads and folds, depending on a reduced number of papillae, and being adaptations to life on the ground, on tree trunks, or on very thin twigs.

Relatively few papillae occur in certain species that winter in temperate or cold climates. This means a reduced area of contact with the substrate and is probably important in the heat regulation by reducing the conductive heat flow through the papillae to the substrate.

The pads and folds have a restricted taxonomic value.

CONTENTS

Introduction

Material and methods

General morphology

Description of species

Phylloscopus trochilus - Willow Warbler

Phoenicurus phoenicurus - Redstart

Erithacus rubecula - Robin

Ficedula hypoleuca - Pied Flycatcher

Anthus trivialis - Tree Pipit

Motacilla alba - Pied Wagtail

Corvus corone - Crow

Sturnus vulgaris - Starling

Hirundo rustica - Swallow

Riparia riparia - Sand Martin

Delichon urbica - House Martin

Alauda arvensis - Sky Lark

Plectropeanx nivalis - Snow Bunting

Regulus regulus - Goldcrest

Certhia familiaris - Tree Creeper

Comparison of species

Discussion

Literature

INTRODUCTION

The plantar surface of passerine species consists of pads and folds separated by furrows. The pads are furnished with papillae, whereas the folds might have or might lack papillae. There is very little published information on the pattern of pads and folds in the passerine species (Blaszyk 1935, Rüggeberg 1970). The present study is a detailed description of pads and folds in 15 species and a comparison with a further 47 species that represent 18 families or subfamilies in the suborder Oscines. A basic pattern of pads and folds is recognized, and the value of pads and folds as a taxonomic character is discussed.

MATERIAL AND METHODS

Most of the birds were collected during the autumn migration at Ottenby Bird Station, Öland in the South Baltic, and the remainder in Skåne, South Sweden. The feet were fixed in Bouin's mixture or a mixture of 80 per cent alcohol, concentrated formol, and concentrated acetic acid (18:1:1). Table 1 shows the species and number of investigated birds. The Vaurie (1959) classification is followed. The individual variation in pads and folds was thoroughly studied in six species, and this material includes drawings of living birds. Both left and right foot were examined in the fixed preparations but only one foot in the living birds. The examinations were made through a stereo microscope, supplied with a camera lucida apparatus for drawing diagrams. Feet of birds from fourteen species were

embedded in celloidin, cut at 40-60 μ m, and stained with Ehrlich's haematoxylin for the study of pads, folds, papillae, and furrows in histological preparations.

GENERAL MORPHOLOGY AND TERMINOLOGY

Fig. 1 shows the plantar surface of a Phylloscopus trochilus. The pads and folds are separated by furrows. The pads are furnished with papillae with an irregular, often pentagonal or hexagonal, contour. Some of the folds have one or two rows of papillae, others have a smooth surface.

Fig. 2 shows a sagittal section through the fourth digit of Phylloscopus trochilus. The digit is fixed in a straightened position so that the furrows are visible. Four pads are shown in the figure, each of them lying close to a phalanx. Between the two distal pads, there are two folds with papillae. A third and smaller fold has no papillae.

The pads and folds in both fixed preparations and living birds are pictured diagrammatically (see Fig. 2). Each pad and fold is surrounded by a line; the space in between represents the furrow. The position of pads and fold was determined in relation to the phalanges and the joints. The joints were located by dissection or by bending the digit. The position of joints is indicated by black areas at the sides of the digit in the diagram.

A furrow is stated from two criteria. When there is a furrow, the papillae should be separated by a gap which opens and closes as the digit is flexed and extended (Fig. 3).

The pads and folds were examined from the top of the digit to the base. Therefore, a proximal sequence of pad designation was adopted. The designation of pads, phalanges, and joints in the present study follows that used in the study of chick embryos (p. 9). Fig. 2 shows the principles. The distal phalanx of the fourth digit is numbered 1, and the phalanx designated phalanx IV:1. The Roman numeral refers to the digit, the Arabic to the phalanx. The joint between phalanges is designated according to the participating phalanges. The distal joint in the fourth digit is designated joint IV:1/2.

There are thirteen pads in the sole of Phylloscopus trochilus (Fig. 1): pad I:1, I:2, II:1, II:2, II:3, III:1, III:2, III:3, IV:1, IV:2, IV:3, and IV:4. In the middle of the foot, ventral to the trochleas of tarsometatarsus, there is a large pad designated central pad. There is no pad at phalanx III:4 or phalanx IV:5.

The occurrence of certain furrows and folds shows an individual variation. A fold in one bird might be lacking in another, or a furrow might subdivide a pad in one bird, but be lacking in another. This individual variation was thorough-

ly studied in six species, including Phylloscopus trochilus (Fig. 4). The plantar surface is divided into regions that have two, three, or four types of pad and fold morphology. The percentual occurrence of each type was calculated.

The left and the right foot from the same bird were examined in the fixed material. Both feet are usually similar. But if the left foot has one type and the right foot another type, this was taken into account in the calculation of the percentual occurrence of the types.

DESCRIPTION OF SPECIES

Phylloscopus trochilus (Fig. 4)

DIGIT I. Between pad I:1 and pad I:2, there are usually two folds; one or three folds occur exceptionally. Pad I:2 has a broad proximal end.

DIGIT II. Between pad II:1 and pad II:2, there are two or three folds, exceptionally only one fold. The fold at joint II:2/3 is lacking in rare cases. There is always one fold proximal to pad II:3.

DIGIT III. Between pad III:1 and pad III:2, there are one or two folds, although three folds or no fold occur exceptionally. The fold at joint III:2/3 is lacking exceptionally. At joint III:3/4 and phalanx III:4, there are one, two, or three folds, three folds being the most common type. The distal one of these folds lies at the joint, and the proximal one or two folds, at the phalanx.

DIGIT IV. Between pad IV:1 and pad IV:2, there are usually two folds, whereas one fold occurs in a few birds. The fold at joint IV:2/3 is present, and the fold at joint IV:3/4 is lacking in most birds. Proximal to pad IV:4, there are usually two folds, the distal lying at joint IV:4/5 and the proximal at phalanx IV:5.

Poenicurus phoenicurus (Fig. 5)

DIGIT I. Between pad I:1 and pad I:2, there is one fold, exceptionally two folds or no fold. Pad I:2 is elongated, and the proximal end is about as broad as the distal.

DIGIT II. Between pad II:1 and pad II:2, there are one, two, three, or four folds. Pad II:2 is substantially broader in the proximal end than in the distal end, and the pad is subdivided into one distal and one proxiaml pad; distal pad II:2 is further subdivided into folds in more than 1/3 of the birds. The fold at joint II:2/3 is often lacking. There is always one fold proximal to pad II:3.

DIGIT III. Between pad III:1 and pad III:2, there is one fold which is lacking in exceptional cases. Pad III:2 has a broad proximal end and a narrow distal end; the pad is subdivided by a furrow in about 2/3 birds. Pad III:3 is narrower in the middle than in the distal and proximal ends; the pad is usually subdivided by one furrow, exceptionally by two. Most birds have one fold at joint III:3/4 and one comparatively large fold at phalanx III:4, but the large fold might be subdivided into two folds, or the folds might have fused.

DIGIT IV. Between pad IV:1 and pad IV:2, there are one, two, or three folds, two being most usual. The folds at joint IV:2/3 and at joint IV:3/4 are mostly lacking. At joint IV:4/5 and phalanx IV:5, there is one or two folds; when there is only one, the proximal fold is lacking.

Erithacus rubecula (Fig. 6)

DIGIT I. Between pad I:1 and pad I:2, there are usually two folds, but one fold occurs in about 1/3 of the birds and three folds exceptionally. Pad I:2 is elongated.

DIGIT II. Between pad II:1 and pad II:2, there are usually two folds but one or three folds occur in a few birds. Pad II:2 is never subdivided. The fold at joint II:2/3 is usually present. Proximal to pad II:3, there is usually one fold but it may be divided into two folds or be lacking.

DIGIT III. Between pad III:1 and pad III:2, there is mostly one fold, exceptionally two folds or no fold. The fold at joint III:2/3 is exceptionally lacking. Pad III:3 is subdivided by a furrow into two portions in rare cases. At joint III:3/4 and phalanx III:4, there are usually two folds, the proximal exceptionally being divided into two folds.

DIGIT IV. Between pad IV:1 and pad IV:2, there are usually two folds but one or three folds also occur. The fold at joint IV:2/3 is usually present and the fold at joint IV:3/4 usually lacking. The fold at joint IV:4/5 is comparatively large; the fold proximal to this is lacking in about 1/5 of the birds.

Ficedula hypoleuca (Fig. 7)

DIGIT I. Between pad I:1 and pad I:2, there are two folds in most birds, one fold in about 1/4, and three folds in rare cases. Pad I:2 is comparatively large and slightly broader at the proximal end.

DIGIT II. Between pad II:1 and pad II:2, there are two, three, or four folds. The fold at joint II:2/3 is lacking in about 1/4, and the fold proximal to pad II:3 is lacking in about 1/10 of the birds.

DIGIT III. Between pad III:1 and pad III:2, there is one fold, exceptionally two folds. Pad III:2 is broader in the proximal than in the distal end, and the pad is subdivided by a furrow in about 1/4 of the birds. The fold at joint III:2/3 is lacking in about 1/10 of the birds. Pad III:3 is subdivided in about half the number of birds. At joint III:3/4 and phalanx III:4 there are one or two folds, exceptionally three folds.

DIGIT IV. Between pad IV:1 and pad IV:2, there are mostly two folds, but one or three folds also occur. The folds at joint IV:2/3 and joint IV:3/4 are mostly lacking. At the base of the digit there are mostly two folds, one fold in about 1/3 of the birds.

Anthus trivialis (Fig. 8)

DIGIT I. Between pad I:1 and pad I:2, there is one fold but the fold is lacking in about 1/3 of the birds. Pad I:2 is very long and elongated.

DIGIT II. Between pad II:1 and pad II:2, there is one fold, in a small number of birds two folds. Pad II:2 is always subdivided in one broad proximal and one narrow distal pad. The fold at joint IV:2/3 is lacking in 1/10 of the birds. Proximal to pad II:3, there are one or two folds but the fold is lacking in a small number of birds.

DIGIT III. Between pad III:1 and pad III:2, there is one fold, exceptionally two folds, or the fold is lacking. Pad III:2 is always subdivided into one broad proximal part and one narrow distal part. The fold at joint III:2/3 is mostly present. Pad III:3 is subdivided into two parts in about 1/4 and into three parts in 3/4 of the birds. There is always one fold at joint III:3/4. Proximal to this fold there is one large or two small folds.

DIGIT IV. Pad IV:1 and pad IV:2 are separated by one fold, which is lacking in 1/10 of the birds. Pad IV:2 is subdivided in 90 per cent of the birds, distal pad IV:2 being more narrow than proximal pad IV:2. The fold at joint IV:2/3 is mostly lacking. Pad IV:3 is always subdivided. The fold at joint IV:3/4 is present in 3/5 of the birds. Pad IV:4 is subdivided into two parts in about 1/3 of the birds. There is always one large fold at joint IV:4/5 and one minor fold at phalanx IV:5.

Motacilla alba (Fig. 9)

DIGIT I. Between pad I:1 and pad I:2, there is one fold, which, however, is lacking in less than half the number of birds. Pad I:2 is elongated.

DIGIT II. Between pad II:1 and pad II:2, there is always one fold. Pad II:2

is always subdivided into one broad proximal and one narrow distal pad. The fold at joint II:2/3 is lacking in the majority of birds. Proximal to pad II:3 there are two or three folds.

DIGIT III. Between pad III:1 and pad III:2 there is one fold, lacking in 1/10 of the birds. Pad III:2 is always subdivided into one broad proximal and one narrow distal pad. The fold at joint III:2/3 is lacking in less than half the number of birds. Pad III:3 is subdivided into two or three parts, the middle appearing as a fold. There is always one fold at joint III:3/4 and two folds, exceptionally one fold, at phalanx III:4.

DIGIT IV. Between pad IV:1 and pad IV:2, there is mostly one fold, two folds or no fold in a few birds. The fold at joint IV:2/3 is lacking in less than half the number of birds, whereas the fold at joint IV:3/4 is lacking in 3/10. The fold at joint IV:4/5 is comparatively large and the fold at phalanx IV:5 is exceptionally lacking.

Sturnus vulgaris (Fig. 10)

DIGIT I. Between pad I:1 and pad I:2, there are two folds, the proximal being much larger than the distal. Pad I:2 has a broad proximal end.

DIGIT II. Between pad II:1 and pad II:2, there is only one fold. Pad II:2 is subdivided by two furrows, and the middle part of the pad has the same appearance as the fold between pad II:1 and pad II:2 or the fold at joint II:2/3. There is one fold proximal to pad II:3.

DIGIT III. Between pad III:1 and pad III:2, there is one fold. Pad III:2 is subdivided into three pads and pad III:3 into two pads. The fold at phalanx III:4 is large.

DIGIT IV. Between pad IV:1 and pad IV:2, there is one fold. Pad IV:2 is subdivided into two pads, one narrow distal and one broad proximal pad. There is one fold at joint IV:2/3 and one at joint IV:3/4. The fold at joint IV:4/5 is large, and appears as a pad.

Corvus corone (Fig. 10)

DIGIT I. Between pad I:1 and pad I:2, there is one comparatively large fold. Pad I:2 has a broad proximal end.

DIGIT II. Between pad II:1 and pad II:2, there is one fold. There is no fold at joint II:2/3 and no fold proximal to pad II:3.

DIGIT III. Between pad III:1 and pad III:2, there is one fold, and there is one fold at joint III:2/3 and one at joint III:3/4.

DIGIT IV. Between pad IV:1 and pad IV:2, there is one fold, but there is no fold at joint IV:2/3 and joint IV:3/4. The fold at joint IV:4/5 has fused with pad IV:4 and with the fold at phalanx III:4.

Hirundo rustica (Fig. 11)

DIGIT I. Between pad I:1 and pad I:2, there are one or two folds. Pad I:2 is long but has a broad proximal end.

DIGIT II. Between pad II:1 and pad II:2, there are one or two folds. Pad II:2 is elongated and pad II:3 comparatively small. There is a fold at joint II:2/3 and a fold proximal to pad II:3.

DIGIT III. Between pad III:1 and pad III:2, there are one or two folds. Pad III:2 is very elongated and it may be subdivided into two pads. There is a fold at joint III:2/3 and a comparatively large fold at joint III:3/4.

DIGIT IV. Between pad IV:1 and pad IV:2, there are one or two folds. There is one fold at each of joint IV:2/3, IV:3/4, IV:4/5, and phalanx IV:5.

Riparia riparia (Fig. 11)

This species has short proximal phalanges in the anterior digits and heavy claws in the first and the third digit.

DIGIT I. Between pad I:1 and pad I:2, there are one or two folds. Pad I:2 is broader at the proximal than at the distal end.

DIGIT II. Between pad I:1 and pad I:2, there is a large fold. Pad II:2 is subdivided into three pads. There is a fold at joint II:2/3. Proximal to this fold there is a small pad.

DIGIT III. Between pad III:1 and pad III:2, there is one or two folds. Pad III:2 is elongated and it may be subdivided into two pads. Pad III:3 is subdivided. There is a fold at joint III:3/4 and a small one at phalanx III:4, though the latter may be lacking.

DIGIT IV. Between pad IV:1 and pad IV:2 there are two folds. There is no fold at joint IV:2/3 and joint IV:3/4 but a large fold at joint IV:4/5.

Delichon urbica (Fig. 12)

Delichon urbica has smaller feet than Hirundo rustica and Riparia riparia. The first digit is relatively shorter. Phalanx II:3, III:4, IV:4, and IV:5 in the proximal parts of the anterior digits are connected by skin and connective tissue. The skin in plantar surface is thin, and some furrows are shallow

and indistinct, particularly those that subdivide the pad.

DIGIT I. Between pad I:1 and pad I:2, there are one or two comparatively large folds. Pad I:2 has a broad proximal end.

DIGIT II. It is uncertain whether there is any fold between pad II:1 and pad II:2. Pad II:2 is subdivided. There is a large fold at joint II:2/3 and another large fold proximal to pad II:3.

DIGIT III. Between pad III:1 and pad III:2, there is one fold. Pad III:2 might be subdivided. There is a large fold at joint III:2/3. Pad III:3 is subdivided. There is a pad at joint III:3/4 and one at phalanx III:4.

DIGIT IV. Pad IV:2 is subdivided. There is a fold at joint IV:2/3, one at joint IV:3/4, and a pad at joint IV:4/5.

Alauda arvensis (Fig. 13)

The digits are slender, and the claw of the first digit is extremely long; the figure does not show the full length. The number of papillae in the sole is low, and some furrows are difficult to state owing to the deep incisions between the papillae which might suggest a furrow. The figure interprets the plantar surface in terms of pads and folds. It differs in some fundamental respects from that in other passerine species.

DIGIT I. Between pad I:1 and pad I:2, there is one fold. Pad I:2 is extremely narrow, and there is a fold proximal to that pad.

DIGIT II. Between pad II:1 and pad II:2, there is one fold. There is a pad at joint II:2/3. It is impossible to determine whether this pad is comparable to a fold or whether it is a proximal part of pad II:2. There are four to five small folds at phalanx II:3.

DIGIT III. Between pad III:1 and pad III:2, there is a fold. At joint III:2/3 there is a pad. This pad can be interpreted as an enlarged fold, but also as a displaced proximal part of pad II:2. There is a comparatively large fold at joint III:3/4.

DIGIT IV. There is one pad at each of joint IV:2/3, IV:3/4, and IV:4/5. Between these pads, there are folds. It is impossible to determine whether these pads correspond to folds in other passerine species, or whether they are displaced pads.

Plectrophenax nivalis (Fig. 14)

The digits are slender and the papillae are few; some are larger than others

The interpretation of the papillae in terms of pads and folds is shown in the figure although some furrows are difficult to verify with certainty.

DIGIT I. Between pad I:1 and pad I:2, there is a fold. Pad I:2 is small.

DIGIT II. Between pad II:1 and pad II:2, there are two folds, the proximal being distal pad II:2. Pad II:2 is subdivided. Proximal pad II:2 is small, comprising only about five papillae. Pad II:3 has about ten papillae, the middle being much larger than the marginal. There is a fold proximal to pad II:3.

DIGIT III. Between pad III:1 and pad III:2, there is one fold. Pad III:2 is subdivided into two pads. Pad III:3 is subdivided into three parts, the distal being the largest and the proximal two appearing as folds. There is one fold at joint III:3/4 and one at the distal part of phalanx III:4.

DIGIT IV. Pad IV:2 is small and appears as a fold. Pad IV:2, IV:3, and IV:4 have some large papillae. There is no fold at joint IV:3/4, but a comparatively large fold at joint IV:4/5.

Regulus regulus (Fig. 15)

The papillae are few, some being substantially larger than others. The difference between pads and folds is gradual. The diagram interprets the plantar surface in terms of pads and folds, but there is an individual variation, particularly in the number of folds between pad 1 and pad 2 in the four digits.

DIGIT I. Between pad I:1 and pad I:2, there are three to six folds. Pad I:2 has few but large papillae, which might represent the middle part of pad I:2 in the other species.

DIGIT II. Between pad II:1 and pad II:2, there are three to five folds. The fold at joint IV:2/3 is small or lacking, but there is a fold proximal to pad II:3.

DIGIT III. Between pad III:1 and pad III:2, there are three to five folds. Pad III:2 is small. Pad III:3 is subdivided into three parts, the distal having one very large papilla.

DIGIT IV. Between pad IV:1 and pad IV:2, there are to folds. Folds at joint IV:2/3 and joint IV:3/4 are small or lacking.

Certhia familiaris (Fig. 16)

The three anterior digits are directed almost parallel to each other. The claws are greatly curved, being adapted to penetrate the bark to tree trunks (Richardson 1942). The digits are compressed from the sides, and the plantar surface is very

narrow. The pattern of pads and folds in this species differs fundamentally from that in the other passerine species. The interpretation of the plantar surface in terms of pads and folds is made in accordance with the morphology of the papillae. In the pads, the papillae have a flat top surface caused by wear against the substrate.

DIGIT I. There is a pad at phalanx I:1 and several folds at phalanx I:2. At the proximal part of the digit, ventral to metatarsus I, the papillae are gathered to a small pad.

DIGIT II. There is a pad at phalanx II:1 and another pad at joint II:2/3. A series of folds lie at phalanx II:2 and one or two folds at phalanx II:3.

DIGIT III. There is a pad at each of phalanx III:1, joint III:2/3, and joint III:3/4, and several folds at phalanx III:2, III:3, and III:4.

DIGIT IV. There is a pad at each of phalanx IV:1, joint IV:2/3, and joint IV:3/4. At joint IV:4/5, there is a fold which is about as large as the adjacent folds. Series of folds lie at phalanx IV:2, IV:3, and IV:4 + IV:5.

COMPARISON OF SPECIES

Phylloscopus trochilus (Figs. 1, 4) has twelve pads in the digits, which are never subdivided. Pad I:2 is broad proximally. Phylloscopus trochilus and Ph. sibilatrix are similar to Ph. trochilus.

The features of Phylloscopus also occur in the examined warbler species of genera Sylvia, Acrocephalus, and Hippolais.

The Grasshopper Warbler Locustella naevia deviates from the other warbler species and has several features comparable to Anthus (Fig. 8): (i) pad I:2 is elongated and narrow proximally; (ii) pad II:2, III:2, and III:3 are subdivided; (iii) pad IV:2 is subdivided into two equally large parts. The features in Locustella naevia indicate relations to the family Motacillidae.

The pattern of Phylloscopus (Fig. 4) occurs in the species of the genera Parus, Bombycilla, Lanius, Fringilla, and Passer; these genera are classified in separate families.

The pads and folds of Corvus monedula, C. frugilegus, and Pica pica are comparable to Corvus corone (Fig. 10). They have thirteen undivided pads and a broad proximal pad I:2. The folds are few. Garrulus glandarius has one fold at each of the joints and two folds between pad I:1 and pad I:2. Concerning the number of folds, Garrulus glandarius seems to be more primitive than the other crow species. It is also regarded as a primitive representative of the

family Corvidae (Amadon 1944).

Phoenicurus phoenicurus (Fig. 5) has pad II:2, III:2, and III:3 subdivided. Pad I:2 is narrow proximally. These features also occur in the species of genera Saxicola, Oenanthe, Luscinia, and Turdus, which are classified in the subfamily Turdinae. Subdivision of the three pads also occurs in Erithacus rubecula (Fig. 6), but the incidence of subdivided pads is low.

Subdivision of pad II:2, III:2, and III:3 occurs in the species of genera Troglodytes, Prunella, and Emberiza, which are classified in different families.

The cardueline species of genera Carduelis, Chloris, Loxia, and Pyrrhula have comparatively few papillae in the pads, which is a differentiation similar to that in Plectrophenax nivalis (Fig. 14), but the pads are not subdivided as in Plectrophenax nivalis. The cardueline species has thus a pattern similar to Fringilla, and this is in conformity with the classification of the cardueline species in the family Fringillidae.

Ficedula hypoleuca (Fig. 7) has pad I:2 broad proximally and narrowing distally; there are two folds at the distal joint of the first, second, and fourth digit. These features are comparable to those in Phylloscopus. Pad III:2 and III:3 are subdivided in a very few birds; this is a feature similar to Phoenicurus phoenicurus.

Muscicapa striata has pads and folds comparable to those in Ficedula hypoleuca (Fig. 7), although the frequencies of different types deviate substantially. Muscicapa striata has most of the papillae larger than Ficedula hypoleuca. The features in the plantar surface justify the separation of the flycatchers in the two genera Ficedula and Muscicapa (Vaurie 1953).

Anthus pratensis has pads comparable to those in Anthus trivialis (Fig. 8). Pad II:2, III:2, and III:3 are always subdivided. Pad IV:2 and IV:3 are subdivided in one broad proximal and one narrow distal part, but the frequency of subdivision is lower in Anthus pratensis than in Anthus trivialis.

Motacilla alba differs from Anthus trivialis in that pad IV:2 and IV:3 are never subdivided in one broad proximal and one narrow distal part. This is obviously related to the comparatively shorter digits in Motacilla alba. Motacilla flava, however, shows a subdivision of pad IV:2 and IV:3.

The subdivision of pad IV:2 and IV:3 in Anthus and Motacilla is not found in any of the examined species of the family Turdidae.

Sturnus vulgaris (Fig. 10) has pad III:2 and III:3 subdivided similar to Phoenicurus phoenicurus (Fig. 5) and pad IV:2 subdivided similar to Anthus trivialis (Fig. 8). Pad I:2 is broad proximally. Pad II:2 is subdivided by two furrows into two pads separated by one fold. This type of subdivision is not found in any other of the examined species. The fold at joint IV:4/5

is large and comparable to that in Anthus trivialis. Thus, Sturnus vulgaris has certain features that distinguish it from the other examined species.

Riparia riparia (Fig. 11) has proximal phalanges in the anterior digits that are shorter than those of Hirundo rustica (Fig. 11), and the folds in these parts of the digits are reduced. This is clearly an adaptation for digging nesting cavities in sand-banks with the feet.

Delichon urbica (Fig. 12) has the proximal parts of the third and fourth digit connected by skin and connective tissue. There are no scales on the digits; instead, there are feathers. The attachments of the skin to the skeletal elements is less firm than in other passerine species; it is brought about by bundles of collagenous fibres that run from the pad directly to the skeletal elements (cf. p. 65). The plantar skin is thin, and many of the furrows are shallow and indistinct, so that the structure is difficult to interpret in terms of pads and folds. However, there is one pad at each phalanx and one fold at each joint, but the folds are much larger than in Hirundo rustica. Thus the general structure of pads and folds in Delichon urbica deviates substantially from that in Hirundo rustica and Riparia riparia (Fig. 11). The general morphology of pads and folds is more like that in Coracias garrulus and Merops apiaster (p. 86) in the Coraciiformes. But this could be due to convergence. Delichon urbica has a fold proximal to pad II:3 and one at phalanx IV:5, which indicate that Delichon urbica is a passerine species. Mayr & Bond (1943) did not recognize any substantial difference between Delichon and the other genera of the family Hirundinidae.

DISCUSSION

The foot in the Passeriformes is characteristic. The first digit is long, directed backward, and not reversible. The three anterior digits are free and the third digit is longest. This foot is adapted for grasping slender branches or twigs in a perching manner.

The passerine species, except Alauda arvensis and Certhia familiaris, has a basic pattern of thirteen pads (Figs. 1, 4, 5, 6, 7, 8, 9, 10, 11). Twelve of these are each related to one phalanx; the thirteenth lies in the central part of the foot, ventral to the trochleas of tarsometatarsus. There are no pads at the proximal phalanx of the third and the fourth digit.

All the examined species have a comparatively large distance between central pad and pad II:3, pad III:3, and pad IV:4 in the proximal part of the anterior digits. The area in between is occupied by one, two, or three folds. This arrange-

ment of pads and folds is related to the grasping of twigs. The passerine birds pinch the twigs with anterior digits above and the posterior digit below in a manner similar to the action of a pair of tongs. The area between the proximal pads of the anterior digits and central pad is then comparable to the hinge in the tongs.

The thirteen pads are undivided in the species of Laniidae, Corvidae, Bombycillidae, Sylviinae, Paridae, Ploceidae, Fringillinae, and Carduelinae (Figs. 1, 4). Subdivision of pad II:2, III:2, and III:3 occurs in the species of Hirudinidae, Motacillidae, Prunellidae, Muscicapinae, Turdinae, and Emberizidae (Figs. 5, 6, 7, 8, 9, 10, 11, 12). Pad IV:2 is subdivided in the species of Motacillidae and Sturnidae, and pad IV:3 in certain species of Motacillidae (Figs. 8, 9, 10). The subdivision occurs in birds that have elongated pads (cf. Anthus trivialis, Fig. 8). It suggests a specialization of the proximal and the distal parts of the pad. Many of the species with subdivided pads have a terrestrial habitat; the birds often frequent the ground. The swallows of the family Hirundinidae are exceptions. The species with broad and undivided pads have arboreal habitats, the birds more rarely visiting the ground. The crows of family Corvidae are exceptions. The narrow and subdivided pads are therefore obviously adapted to habitats that include the ground.

The folds separate the pads, and facilitate a more intense bending of the digit (Fig. 3). They show an individual variation in occurrence (Fig. 4, 5, 6, 7, 8, 9). From the comparison of species, it is possible to recognize a basic pattern of folds.

There are two types of folds: one lies at the joints (Fig. 12). There is one fold at each joint I:1/2, II:1/2, III:1/2, and IV:1/2. This fold might exceptionally be lacking (Fig. 5, 6, 8, 9). These folds are homologous with similar folds in certain non-Passeriformes. The fold at joint II:2/3, III:2/3, III:3/4, IV:2/3, IV:3/4, and IV:4/5 occurs in all examined species, except certain crows, but some are present in low frequency or in rare cases (Fig. 4, 5, 6, 7, 8, 9). These folds correspond to pads in certain non-Passeriformes and can be regarded as reduced pads. The reduction of the pads to folds is related to the intense bending of the digits (Fig. 3).

The second type of folds comprises the remaining folds. They are discussed in relation to Fig. 17.

Fold A occurs in certain species (Fig. 4, 5, 6, 7, 10, 12, 15). The individual variation shows that when the fold is lacking, the adjacent pad I:2 is larger. Therefore it is concluded that the fold is a separated part of pad I:2.

Fold B occurs in certain birds (Fig. 4, 5, 6, 7, 10, 15). Two or three folds might occur in this region (Fig. 4, 5, 6, 7, 15). When the folds are present,

pad II:2 is reduced in size. It is concluded that fold B is a separated part of pad II:2.

Fold C occurs in all the examined species, although it may be lacking in certain individuals (Fig. 6, 7, 8, 10) or it may be divided into two folds (Fig. 8, 9). It is a characteristic feature for the examined species of Passeriformes. It is interpreted as a separated part of pad II:3.

Fold D occurs in several species (Fig. 4, 5, 6, 7, 8, 15). It is exceptional to find two folds in this region (Fig. 4, 6, 15). When the fold is lacking, pad III:2 extends distally. It is concluded that fold D is a separated part of pad III:2.

Fold E. Several species have one large fold in this region (Fig. 5, 6, 8, 10), whereas other species have two (Fig. 4, 9). These folds might fuse with the adjacent fold at joint III:3/4 (Fig. 4, 5, 7), but this is exceptional. The corresponding site at phalanx III:4 in certain non-Passeriformes is occupied by a pad. It is concluded that fold E is homologous with that pad. The reduction of the pad to a fold is related to the pinching method of grasping twigs (described above, Fig. 3).

Fold F occurs in several species (Fig. 4, 5, 6, 7, 8, 9, 15). It might be divided into two folds (Fig. 4, 5, 6, 7). The conclusion is that it is a separated part of pad IV:2.

Fold G is present in all examined species, but is always small. It lies at phalanx IV:5. The comparable site in certain non-Passeriformes is occupied by a pad. It is therefore concluded that this fold is a reduced pad. The reduction is related to the pinching manner of grasping twigs.

The folds in the second type (A-G in Fig. 17) are thus interpreted either as reduced phalanx pads or as separated parts of phalanx pads.

Pad II:2, III:2, and IV:2 are subdivided in certain species, as discussed above. This subdivision is related to the specialization of the distal and the proximal part of the pad. This is obviously a feature that differs from the separation of a minor part of the pad into one or two folds (B, D, and F in Fig. 12), related to the bending of the digit. Both these mechanisms, however, can operate at the same time, as seen in pad II:2 of Erithacus rubecula and Ficedula hypoleuca (Fig. 6, 7).

The pads, folds, and papillae in Alauda arvensis, Plectrophenax nivalis, Certhia familiaris, and Regulus regulus are described (Fig. 13, 14, 15, 16). The four species have very few papillae, and the pattern of pads and folds, which is characteristic of most passerine species, has more or less disappeared. Alauda arvensis and Plectrophenax nivalis live on ground and never visit trees. Certhia familiaris climbs on tree trunks, and Regulus regulus frequents very

thin twigs in coniferous woods. The conclusion from the observations on these species is that the basic pattern of thirteen pads is an adaptation to grasp twigs, and that this pattern disappears when twigs are excluded from the habitat.

Regulus regulus has a low number of papillae (Blaszyk 1935); this is possibly an adaptation to thin twigs, but is also correlated with a small body. Few papillae are also a feature in Aegithalos caudatus (Blaszyk 1935) and the cardueline species examined in the present study. Alauda arvensis, Plectrophenax nivalis, and Certhia familiaris have also few papillae, although these species have different habitats.

A probably important functional implication of the few papillae concerns heat regulation. The low number of papillae reduces the contact with the substrate, which could reduce the small but inevitable heat flow through the papilla to the substrate (discussed on p.106). All the mentioned birds with few papillae winter in temperate or cold climates, where they are subjected to temperature stress during the winter. None of the species examined in the present study and wintering in tropical Africa have a low number of papillae.

The species comparisons show that the pads and folds have a restricted value as taxonomic character. The differences between Locustella and Phylloscopus-Sylvia-Hippolais-Acrocephalus and between Delichon and Hirundo-Riparia indicate different relations. The pads and folds in Sturnus have probably a diagnostic value. The morphology of pads and folds, however, might not be used to show relations among families or subfamilies of passerine species. The Passeriformes are considered to be a morphologically uniform group (Stresemann 1959), and the present study supports this conclusion. A basic pattern of pads and folds is deduced (Fig. 17). The subdivision of pads, which is a feature in certain families, might have evolved several times independently, probably in relation to a narrowing and elongation of the pads, which then are specialized in different parts.

LITERATURE

- Amadon, D. 1944. The genera of the Corvidae and their relationships. - Amer. Mus. Novit. 1251:1-21.
- Blaszyk, P. 1935. Untersuchungen über die Stammesgeschichte der Vogelschuppen und Federn und über die Abhängigkeit ihrer Ausbildung am Vogelfuss von der Funktion. - Morph. Jahrb. 75:483-567.
- Mayr, E. & Bond, J. 1943. Notes on the generic classification of the swallows. - Ibis 85:334-341.
- Richardson, F. 1942. Adaptive modifications for tree-trunk foraging in birds. - Univ. California Publ. Zool. 46:317-368.
- Rüggeberg, T. 1960. Zur funktionellen Anatomie der hinteren Extremität einiger mitteleuropäischer Singvogelarten. - Z. wiss. Zool. 164:1-106.
- Stresemann, E. 1959. The status of avian systematics and its unsolved problems. - Auk 76:269-280.
- Vaurie, C. 1953. A generic revision of flycatchers of the tribe Muscicapini. - Bull. Amer. Mus. Nat. Hist. 100:453-538.
- Vaurie, C. 1959. The Bird of the Palearctic Fauna, Passeriformes. Witherby, London.
- Witherby, H.F., Jourdain, F.C.R., Ticehurst, N.F. & Tucker, B.W. 1943. The Handbook of British Birds. Vol. 1. Witherby, London.

Table 1. Species and number of investigated birds. L after the number indicates that a drawing was made from a living bird. The classification and taxonomy of Vaurie (1959) is followed, but the scientific names of cardueline species are in accordance with Witherby et al. (1943). An asterisk (*) indicates that the foot was studied in histological preparations.

Hirudinidae	Phylloscopus trochilus - 54+101L *
Riparia riparia - 2,	Phylloscopus collybita - 5
Hirundo rustica - 10, *	Phylloscopus sibilatrix - 20
Delicon urbica - 3 *	Regulus regulus - 15 *
Alaudidae	Muscicapidae - Muscicapinae
Erimophila alpestris - 1	Ficedula hypoleuca - 45+28L *
Alauda arvensis - 4 *	Muscicapa striata - 91+50L
Motacillidae	Muscicapidae - Turdinae
Anthus trivialis - 14+28L *	Saxicola rubetra - 1
Anthus pratensis - 3+12L	Oenanthe oenanthe - 3
Anthus cervinus - 1L	Phoenicurus phoenicurus - 111+27L
Motacilla flava - 3	Erithacus rubecula 58+9L *
Motacilla alba - 12+22L *	Luscinia svecica - 5
Laniidae	Turdus pilaris - 1
Lanius collurio - 5 *	Turdus merula - 5 *
Sturnidae	Turdus iliacus - 12 *
Sturnus vulgaris - 14 *	Turdus philomelos - 10
Corvidae	Paridae
Garrulus glandarius - 2	Parus palustris - 10
Pica pica - 4	Parus caeruleus - 18
Corvus monedula - 3	Parus major - 20 *
Corvus corone - 5 *	Certhiidae
Corvus frugilegus - 1	Certhia familiaris - 3 *
Bombycillidae	Ploceidae
Bombycilla garrulus - 3	Passer domesticus - 25
Troglodytidae	Fringillidae - Fringillinae
Troglodytes troglodytes - 15	Fringilla coelebs - 13 *
Prunellidae	Fringillidae - Carduelinae
Prunella modularis - 2	Chloris chloris - 11
Muscicapidae - Sylviinae	Carduelis carduelis - 1
Locustella naevia - 1	Carduelis flammea - 9
Acrocephalus schoenobaenus - 3	Carduelis spinus - 6 *
Hippolais icterina - 2	Loxia curvirostra - 9 *
Sylvia borin - 20	Pyrrhula pyrrhula - 33
Sylvia atricapilla - 18	Emberizidae
Sylvia communis 20	Emberiza citrinella - 1
Sylvia curruca - 20	Emberiza schoeniclus - 5
	Plectrophenax nivalis - 6 *

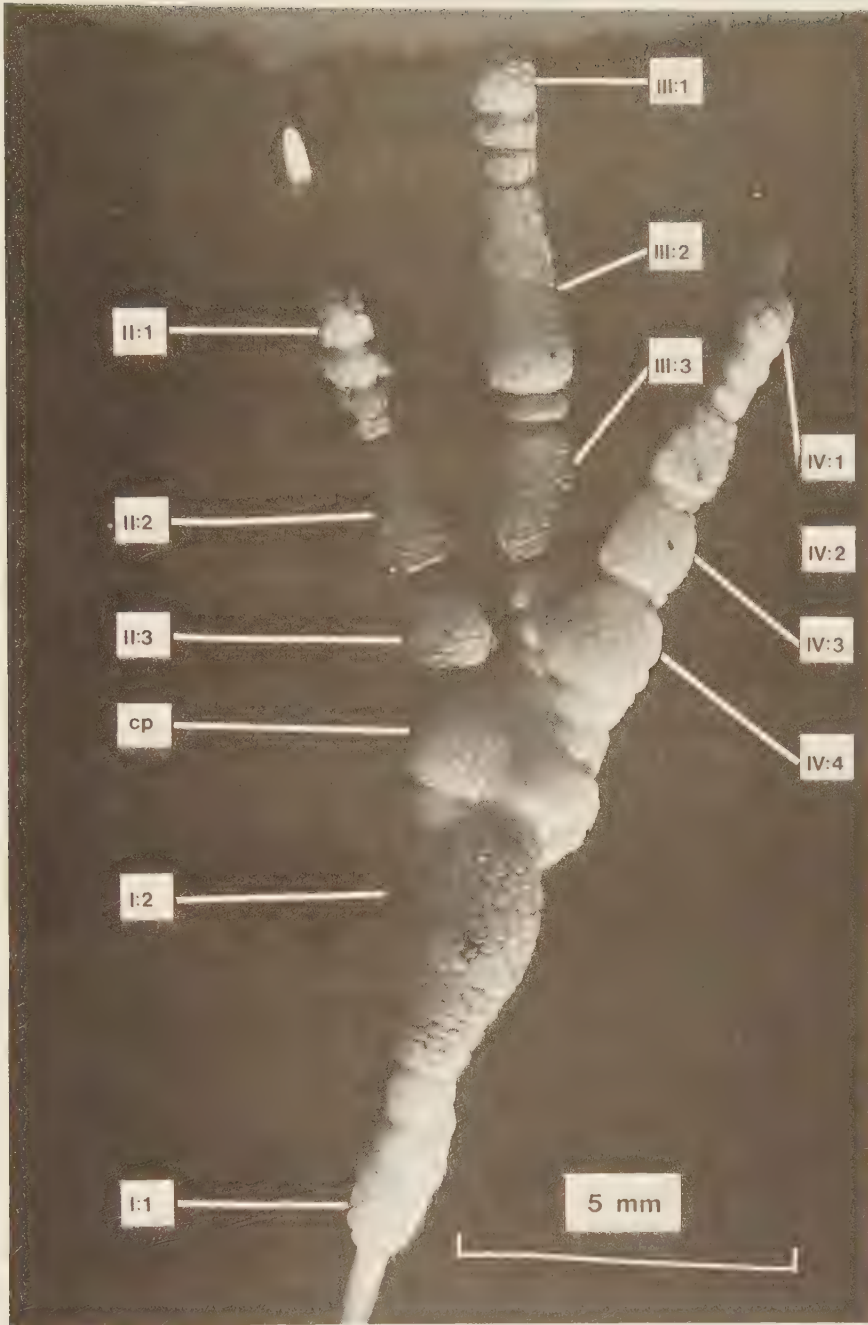


Fig. 1. Plantar surface in Phylloscopus trochilus, showing pads, folds, furrows, and papillae. The thirteen pads are designated.

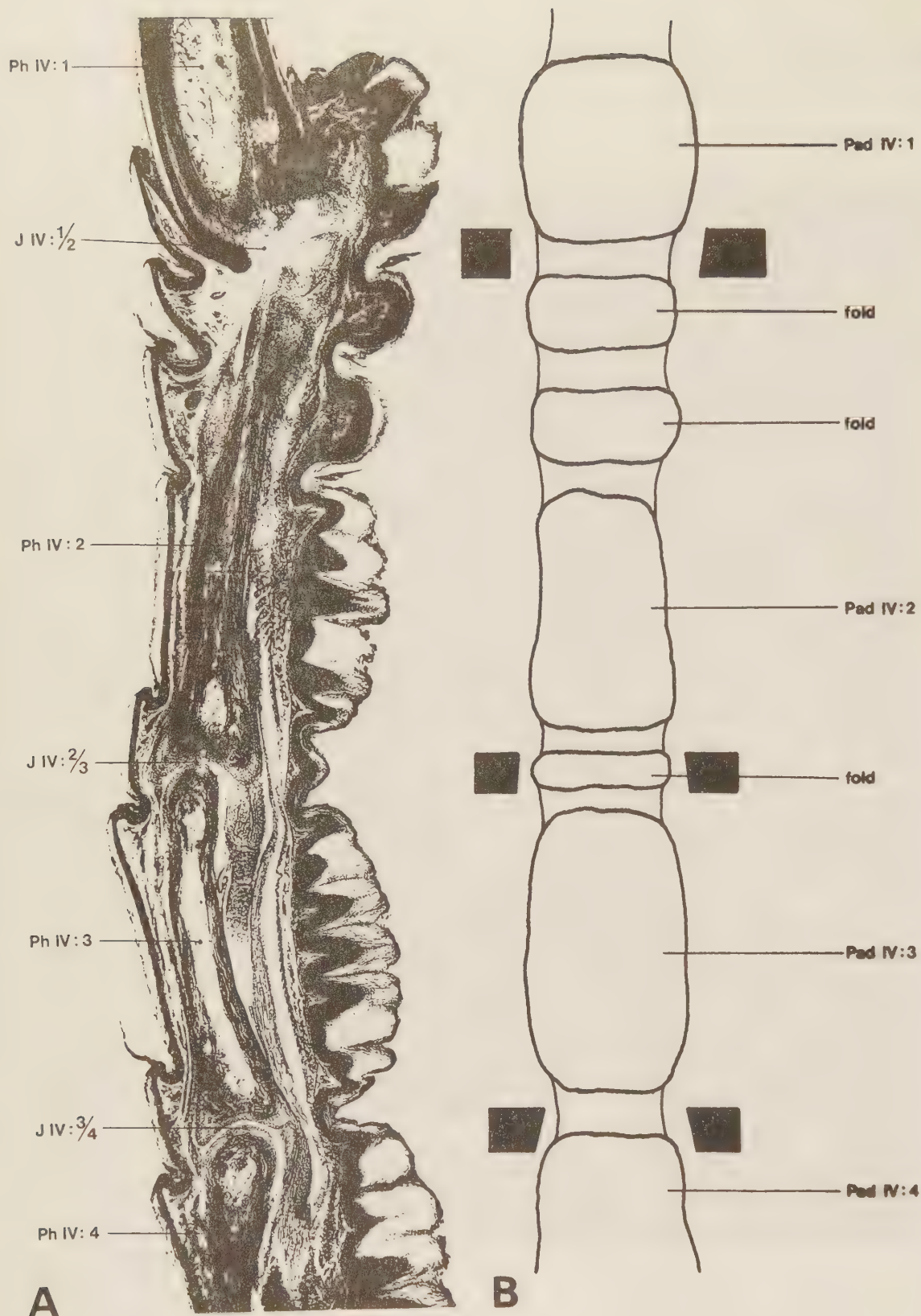


Fig. 2. (A) Sagittal section through the fourth digit in *Phylloscopus trochilus*, showing phalanges, joints, pads, folds, furrows, and papillae. The stratum germinativum is stained dark. Celloidin section, cut at 40 μm and stained with Ehrlich's haematoxylin. (B) Schematic drawing of pads and folds in the same digit. Black areas at the side of the digit indicate the position of joints. Ph, phalanx; J, joint.

A



B



Fig. 3. (A) Extended and (B) bent fourth digit, showing the furrows between the pads and folds opened and closed.

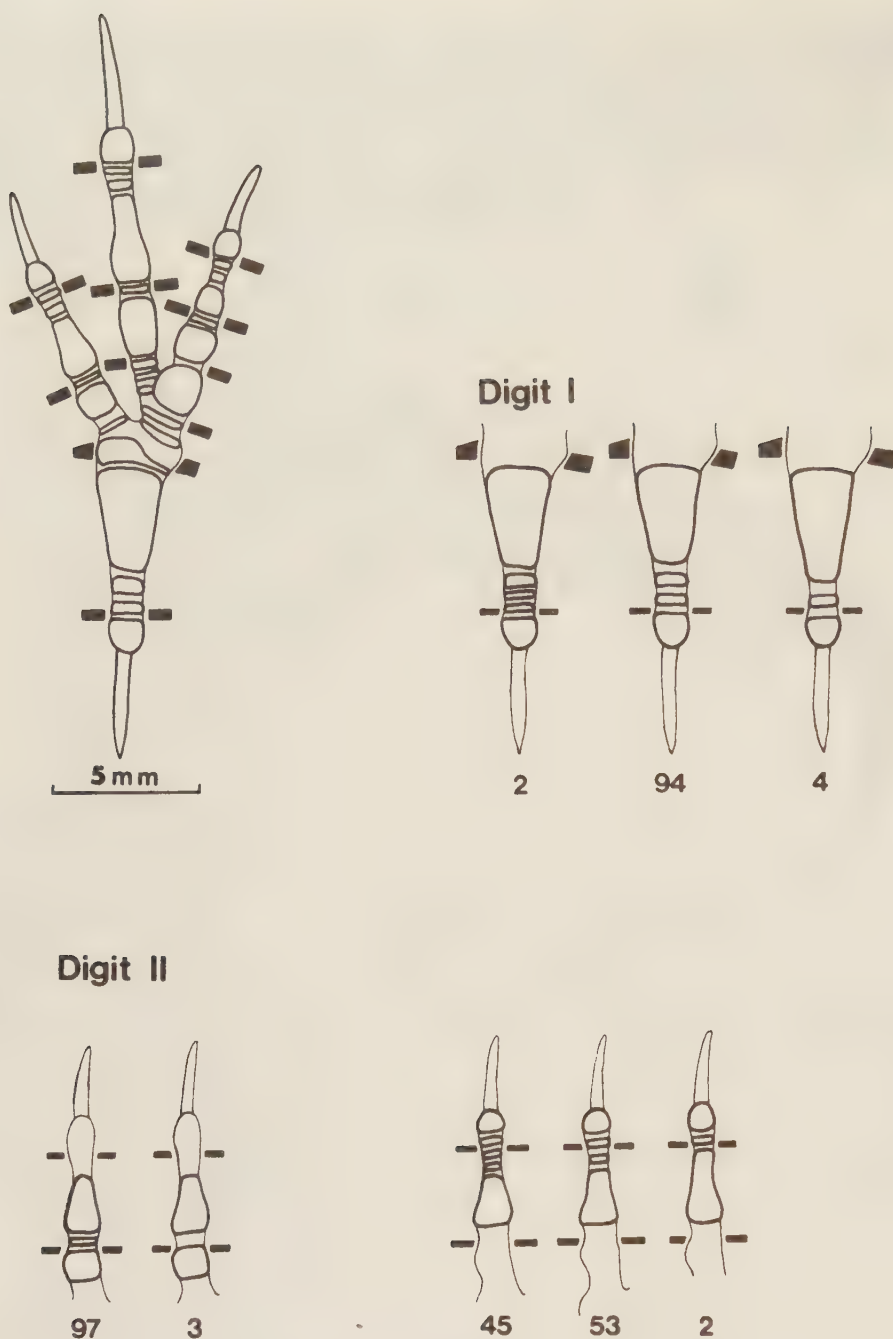
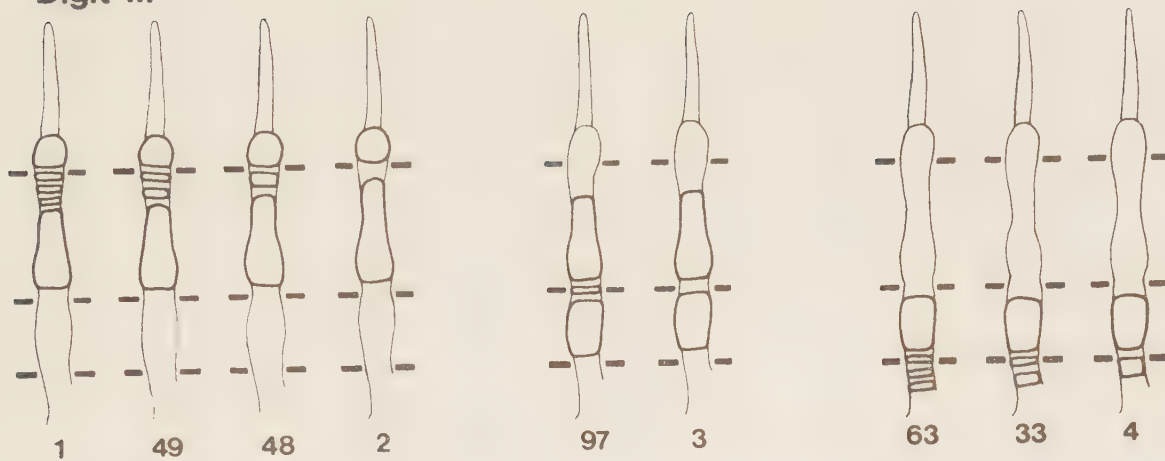


Fig. 4. Pads and folds in Phylloscopus trochilus. The plantar surface is divided into regions, and the types in each region are drawn. The numerals indicate the percentual occurrence of each type; the number investigated is 155. Black areas at the sides of the digits indicate the position of joints.

Digit III



Digit IV

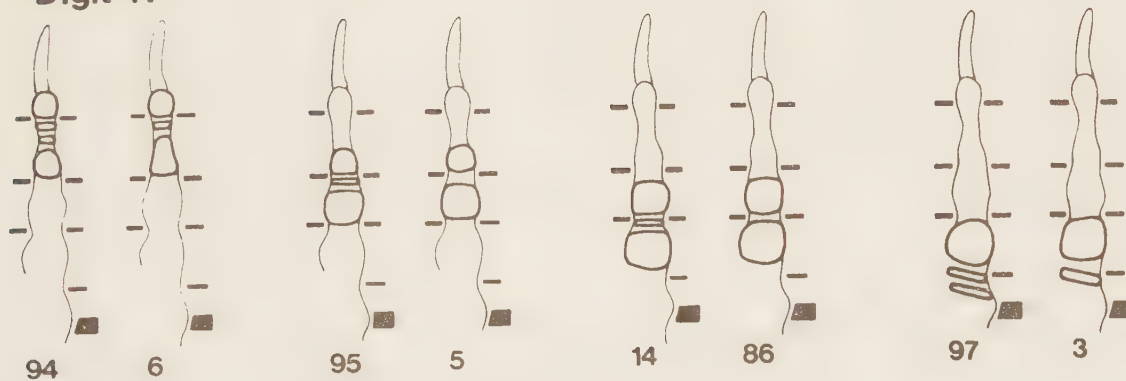


Fig. 4, continued.

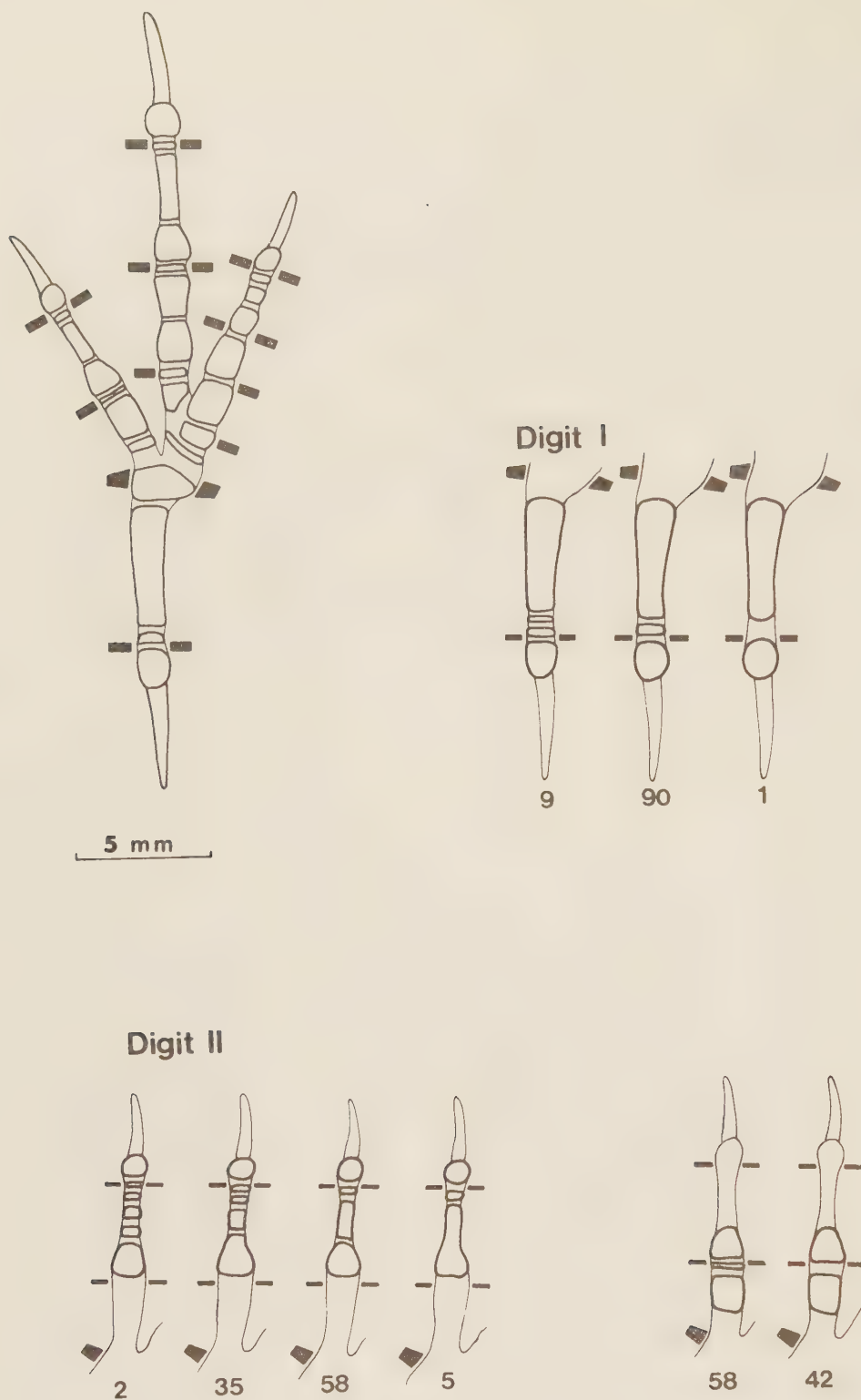
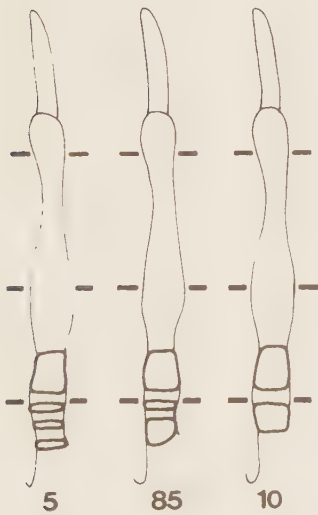
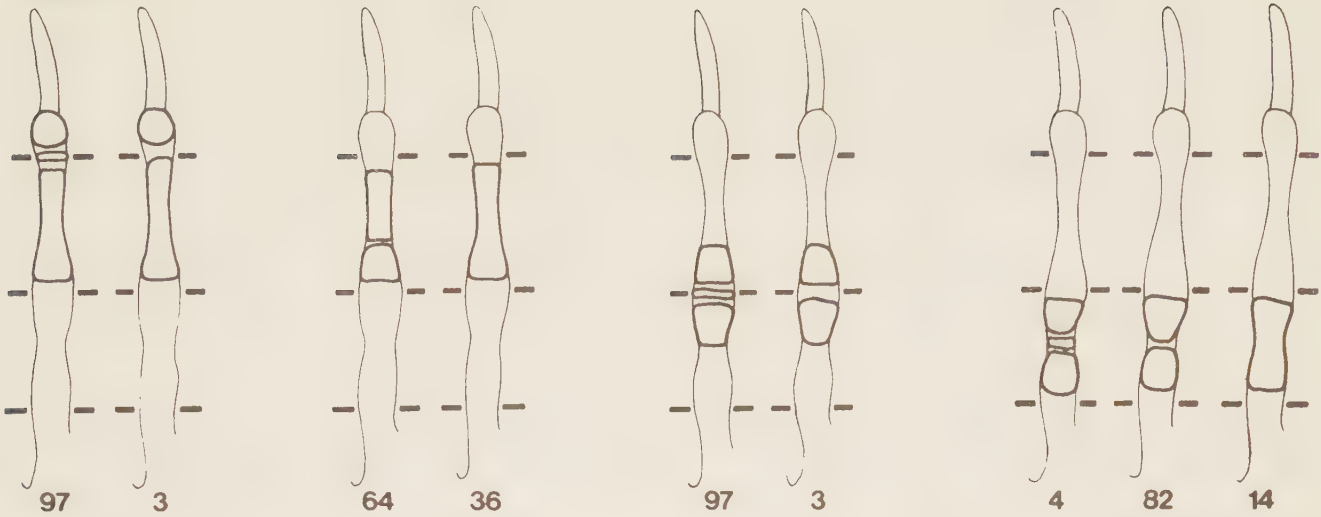


Fig. 5. Pads and folds in Phoenicurus phoenicurus. The plantar surface is divided into regions, and the types in each region are drawn. The numerals indicate the percentual occurrence of each type; the number investigated is 138. Black areas at the sides of the digits indicate the position of joints.

Digit III



Digit IV

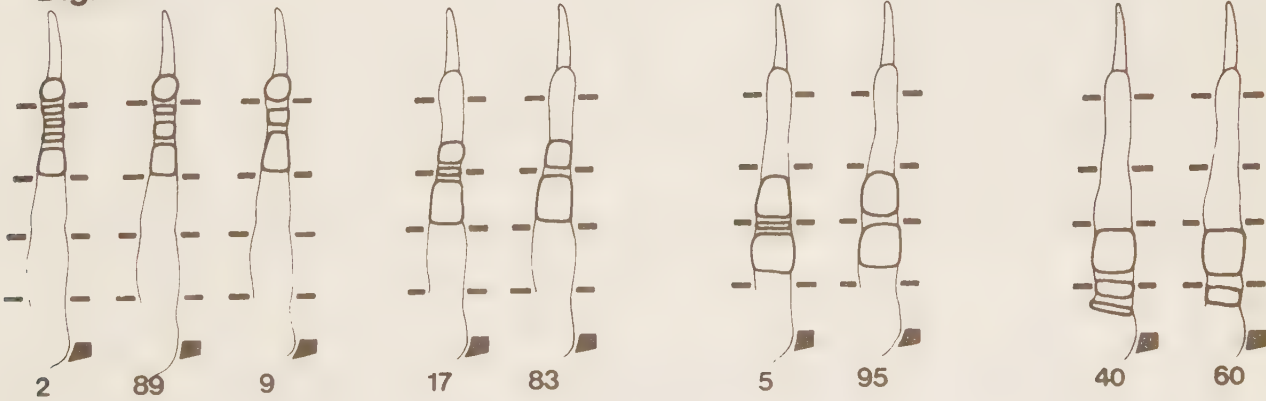
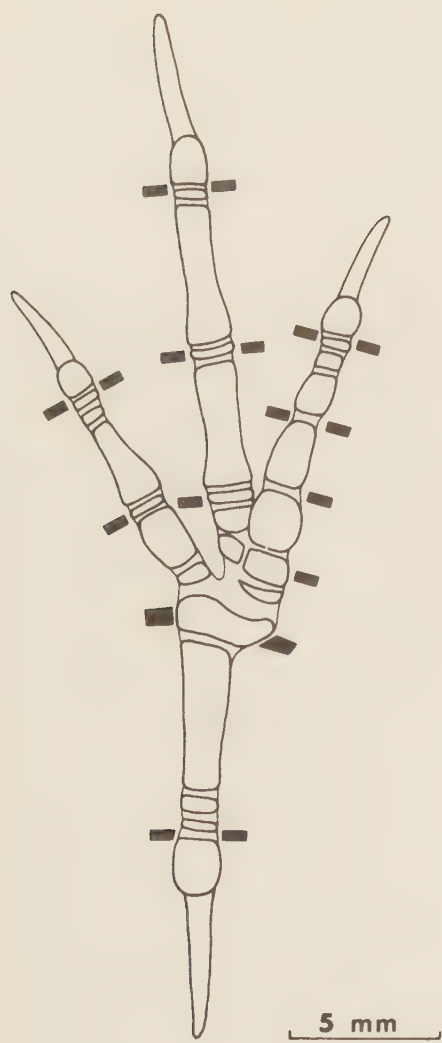
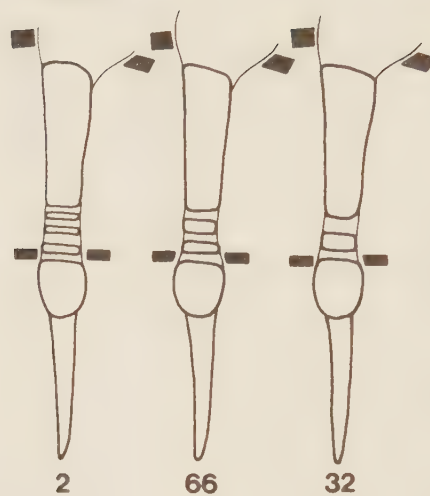


Fig. 5, continued.



Digit I



Digit II

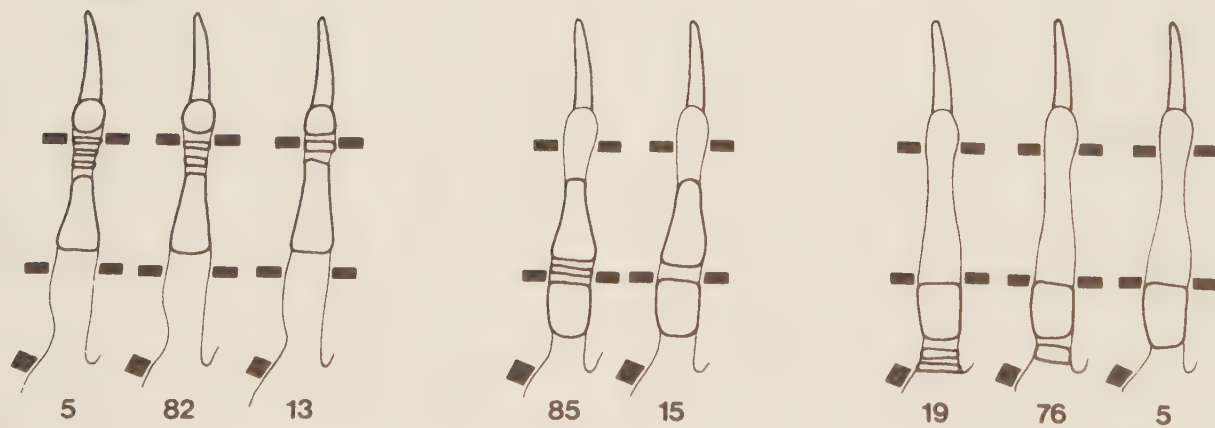
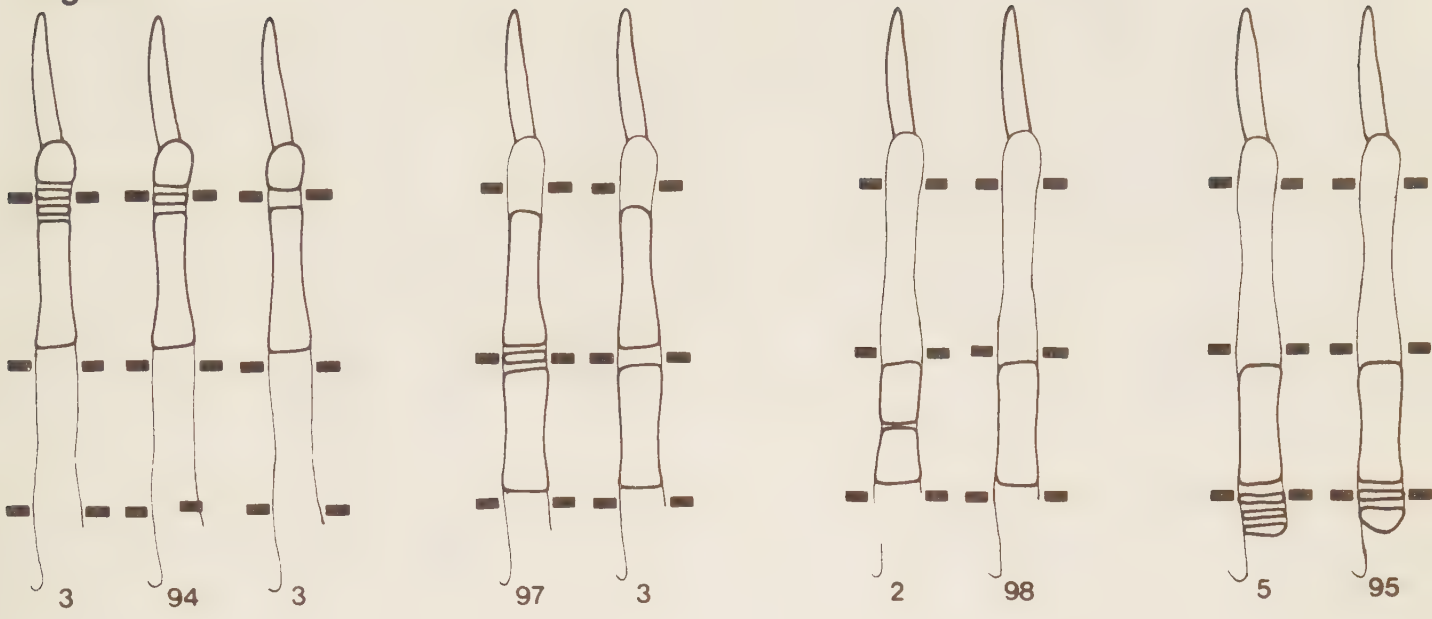


Fig. 6. Pads and folds in Erithacus rubecula. The plantar surface is divided into regions, and the types in each region are drawn. The numerals indicate the percentual occurrence of each type; the number investigated is 67. Black areas at the sides of the digits indicate the position of joints.

Digit III



Digit IV

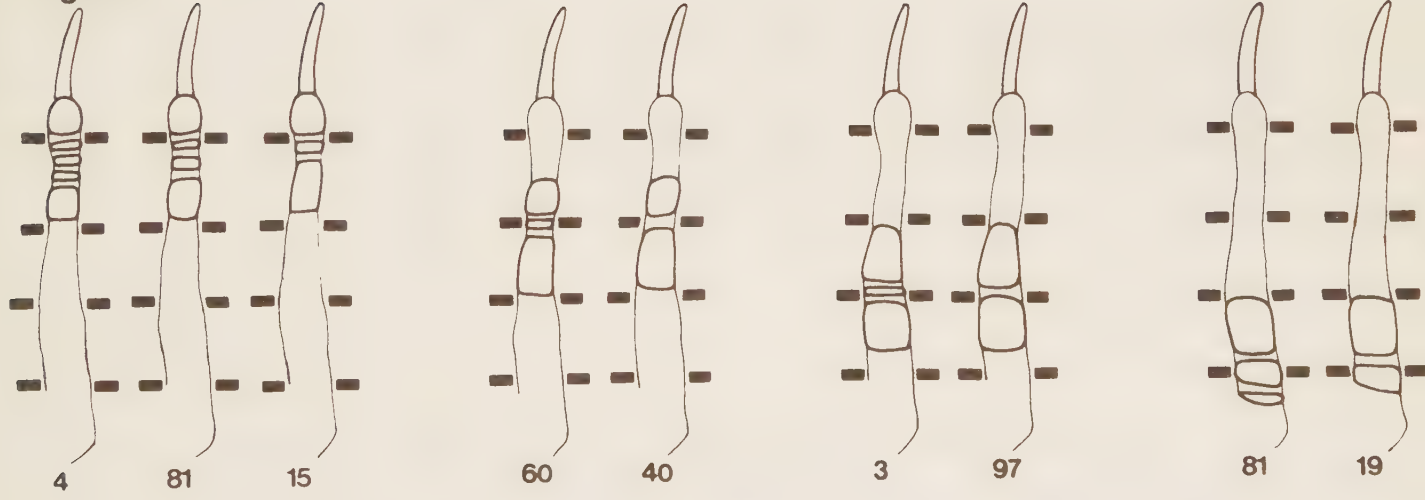
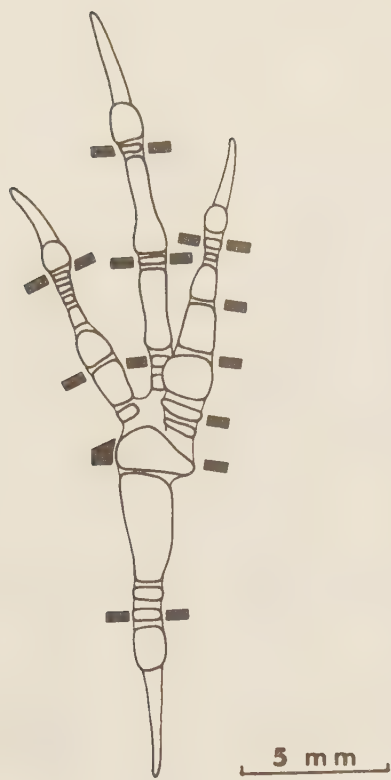
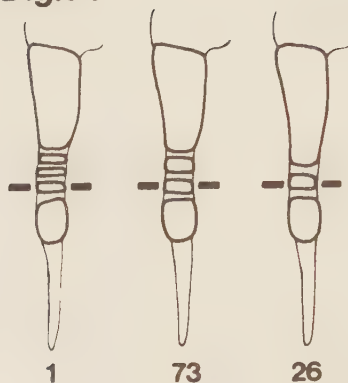


Fig. 6, continued.



Digit I



Digit II

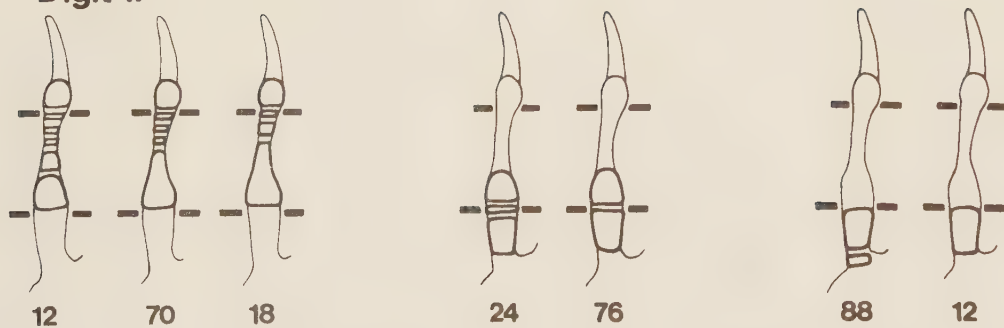
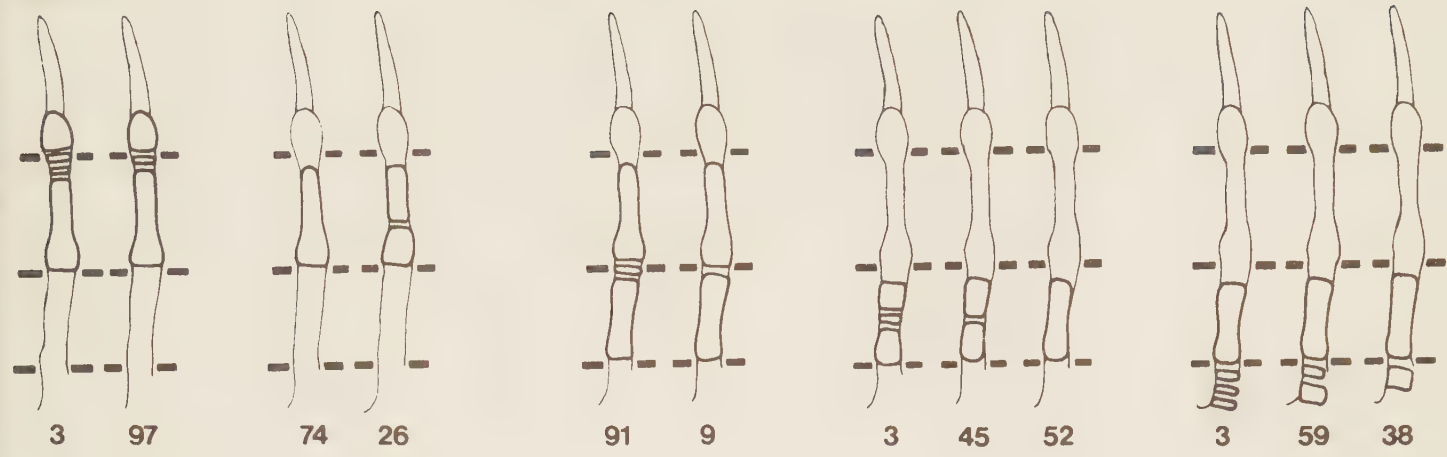


Fig. 7. Pads and folds in Ficedula hypoleuca. The plantar surface is divided into regions, and the types in each region are drawn. The numerals indicate the percentual occurrence of each type; the number investigated is 73. Black areas at the sides of the digits indicate the position of joints.

Digit III



Digit IV

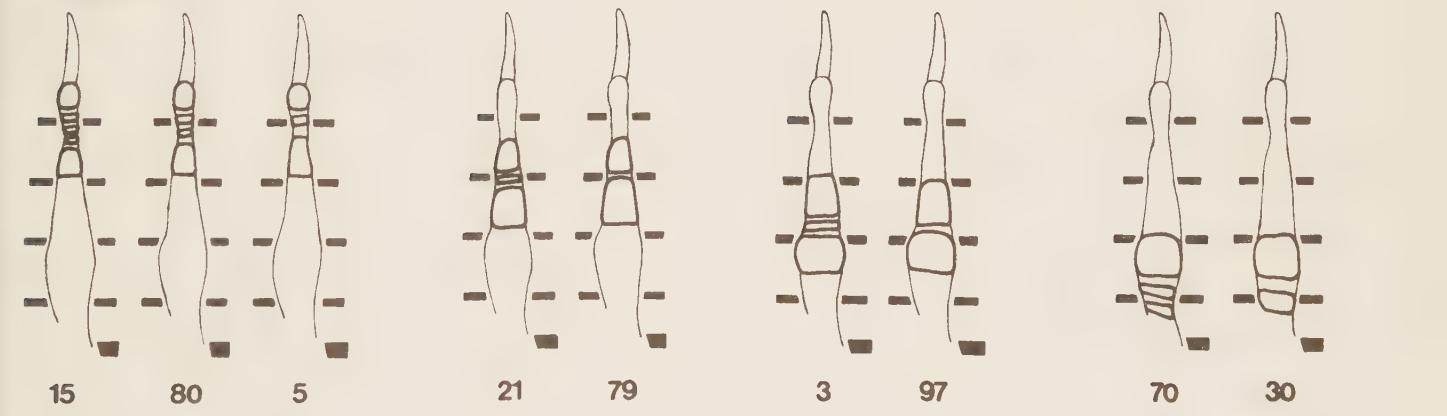


Fig. 7, continued.

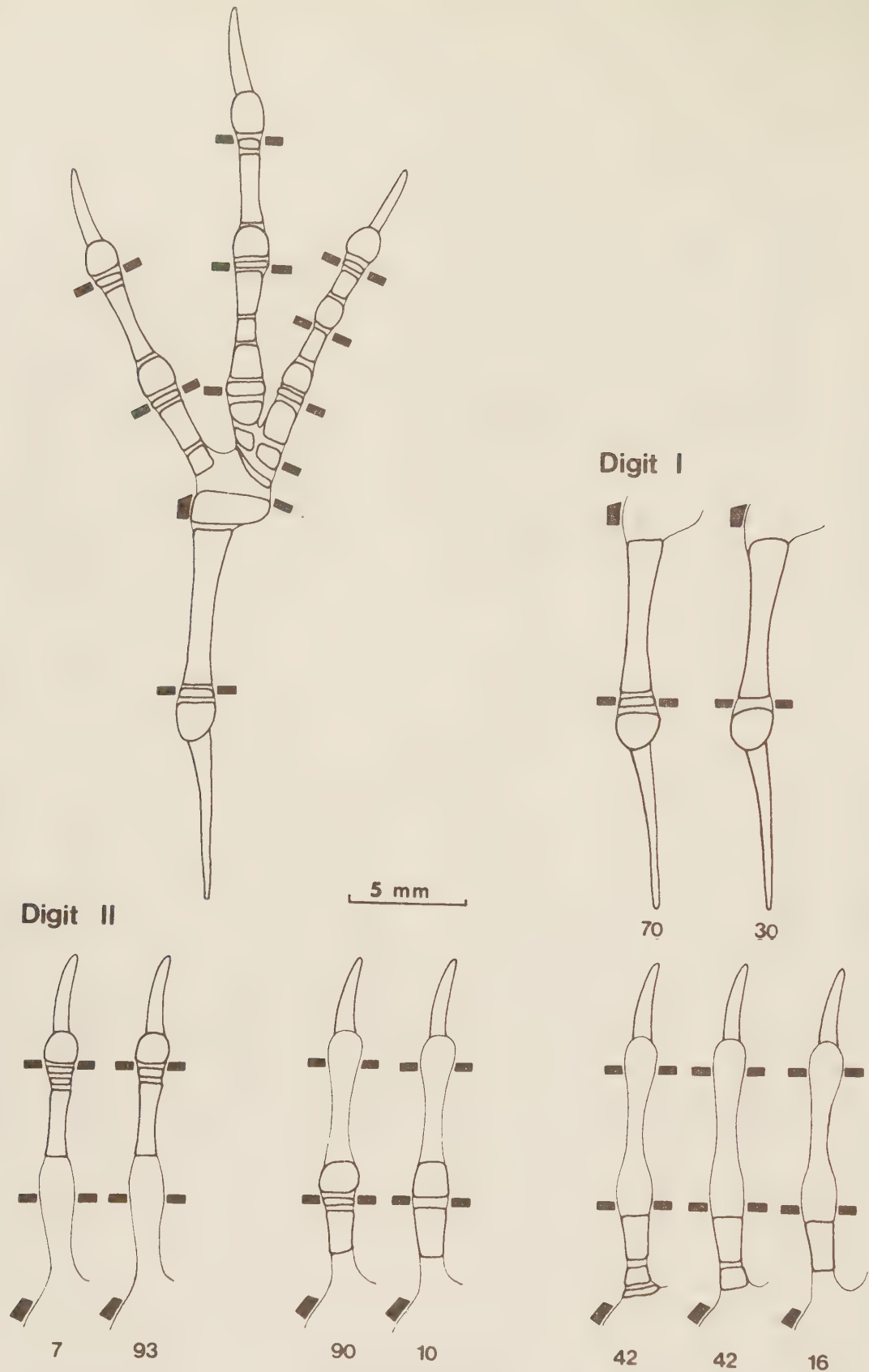
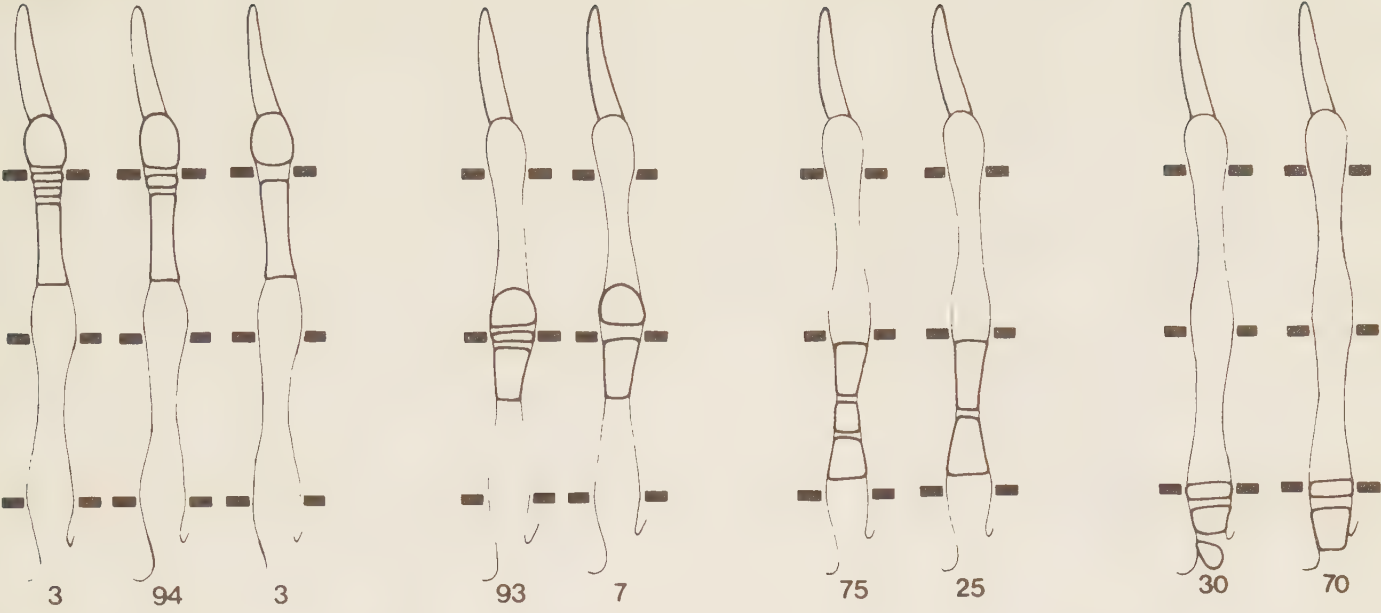


Fig. 8. Pads and folds in *Anthus trivialis*. The plantar surface is divided into regions, and the types in each region are drawn. The numerals indicate the percentual occurrence of each type; the number investigated is 42. Black areas at the sides of the digits indicate the position of joints.

Digit III



Digit IV

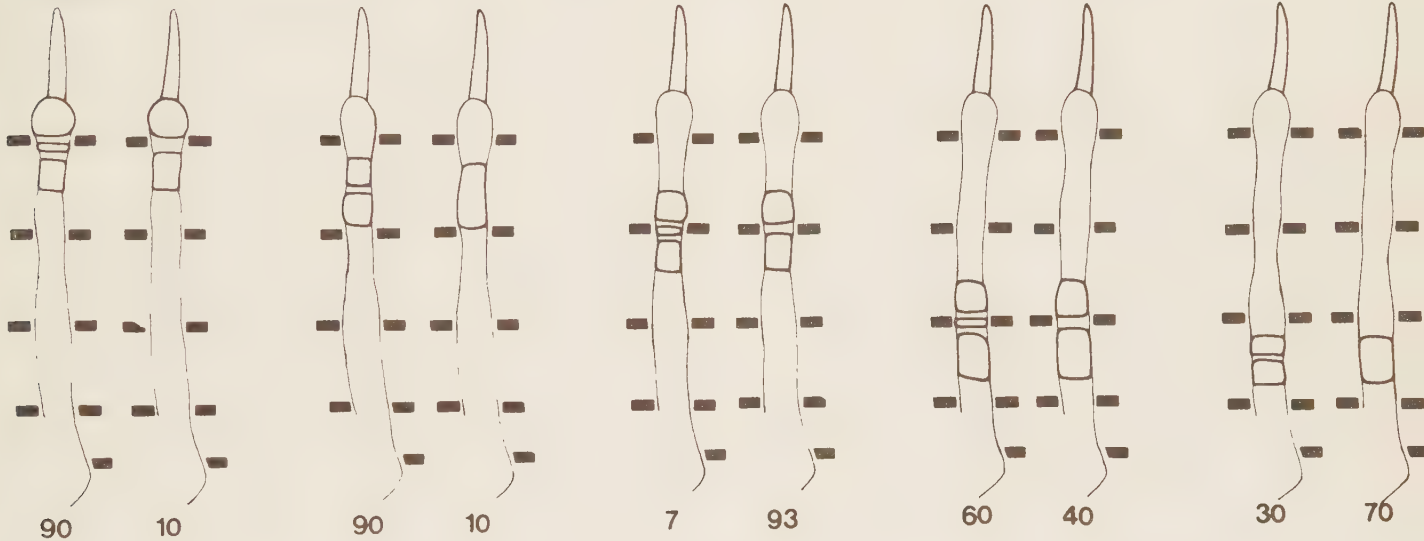


Fig. 8, continued.

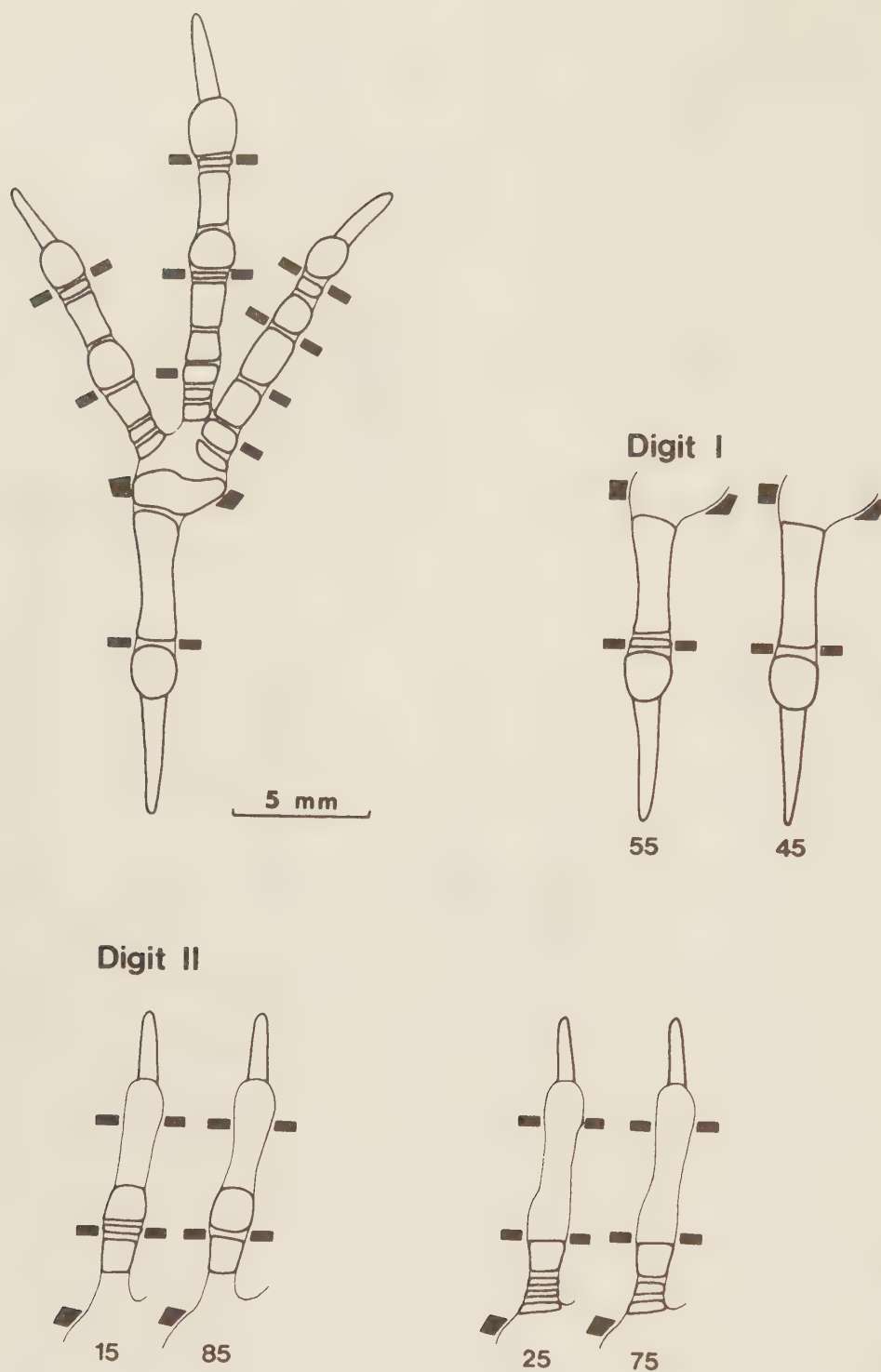
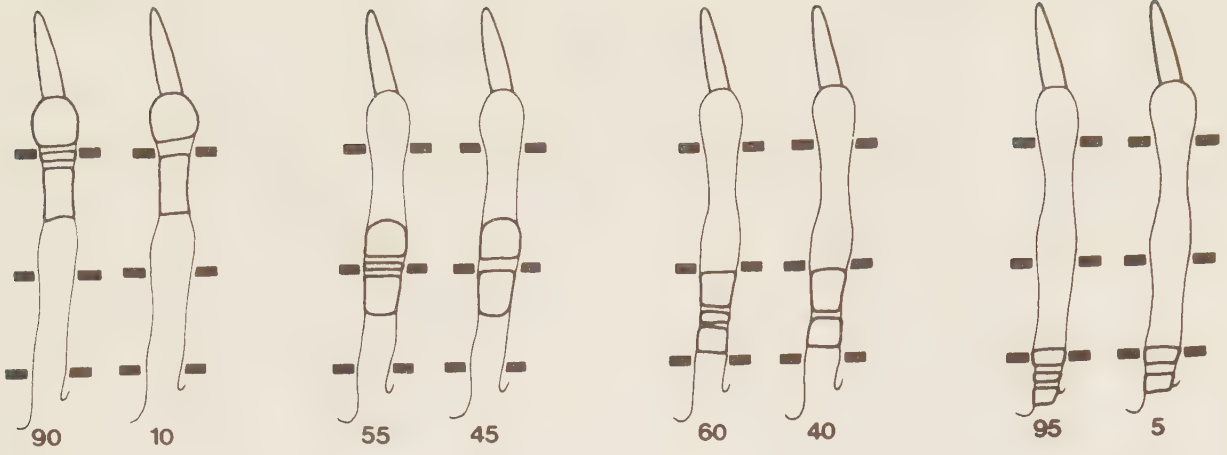


Fig. 9. Pads and folds in Motacilla alba. The plantar surface is divided into regions, and the types in each region are drawn. The numerals indicate the percentual occurrence of each type; the number investigated is 34. Black areas at the sides of the digits indicate the position of joints.

Digit III



Digit IV

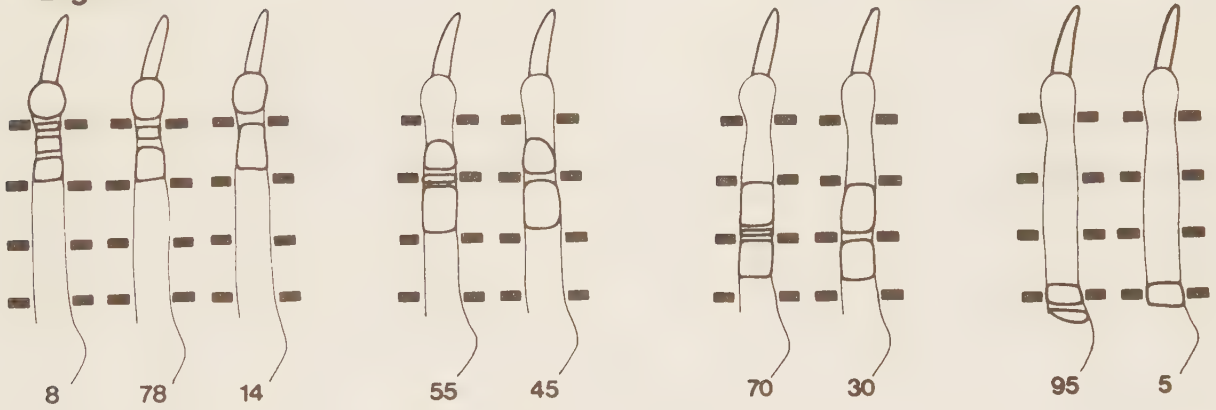


Fig. 9, continued.

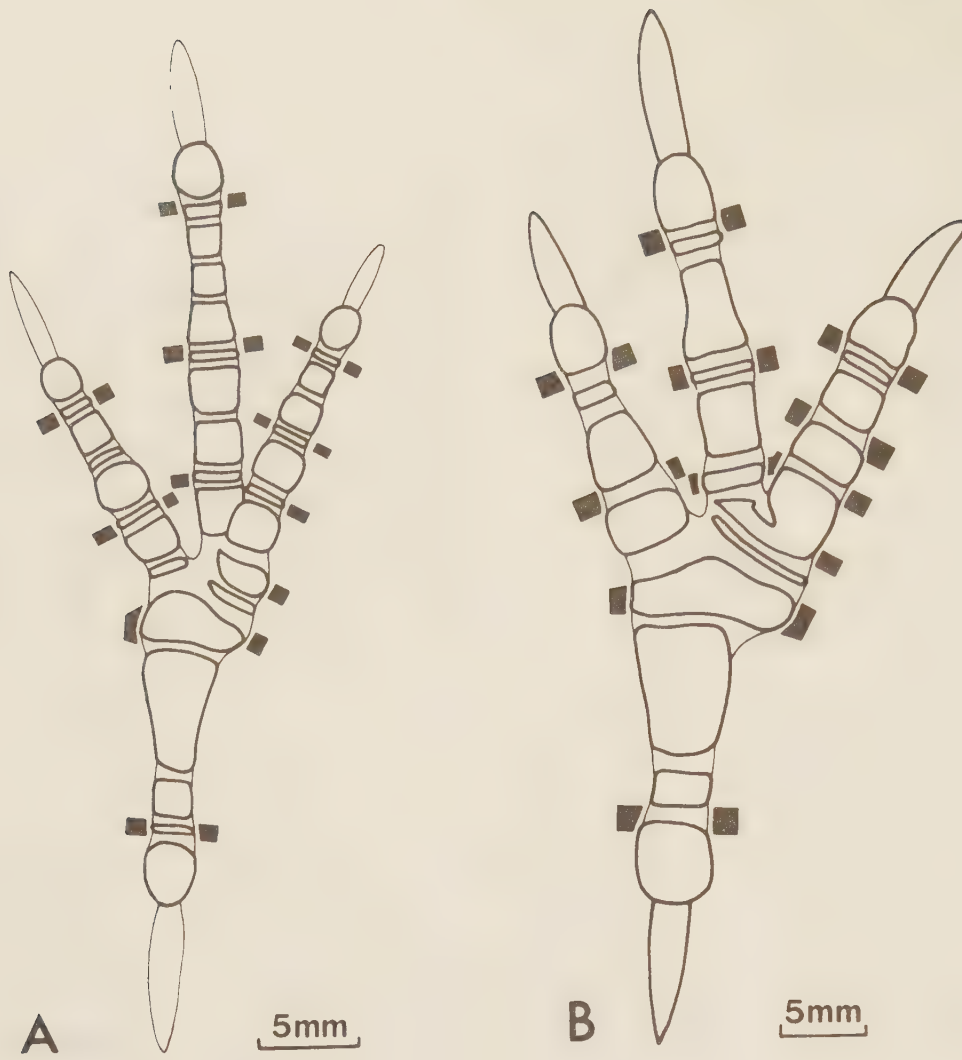


Fig. 10. Pads and folds in (A) Sturnus vulgaris and (B) Corvus corone.

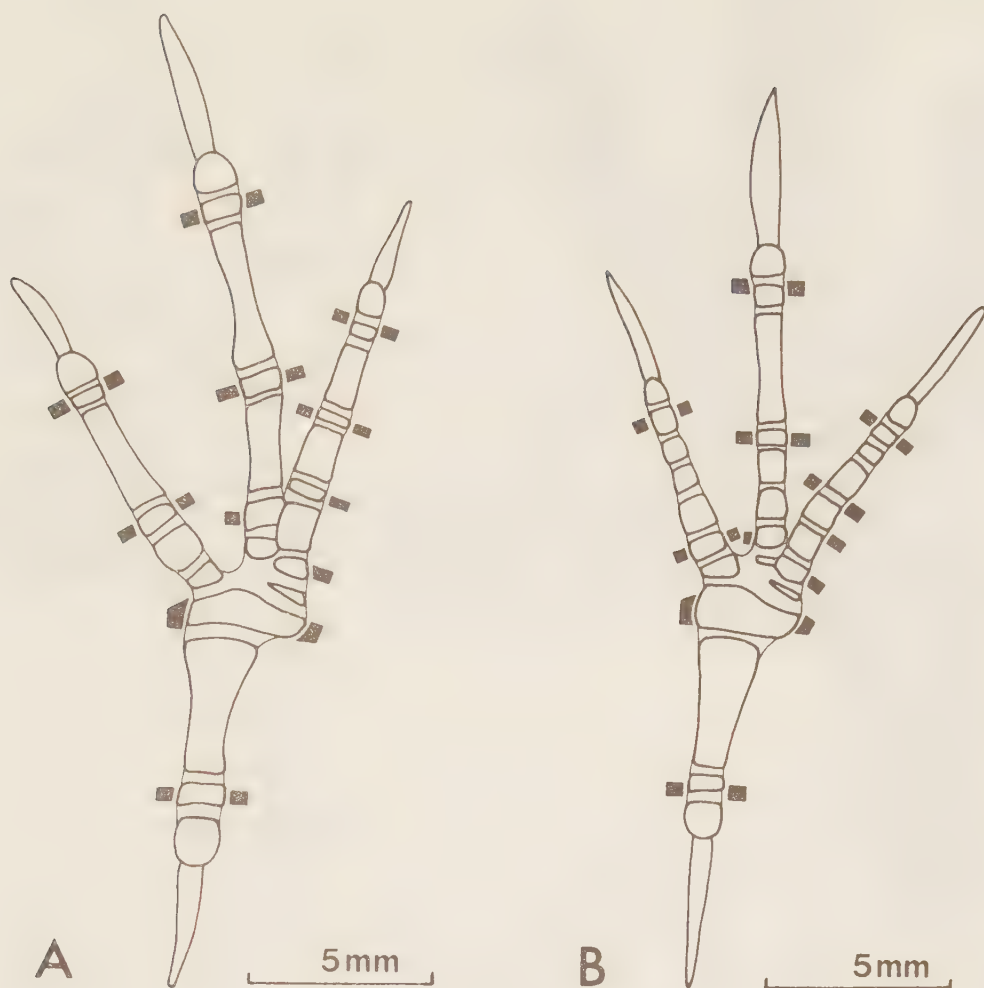
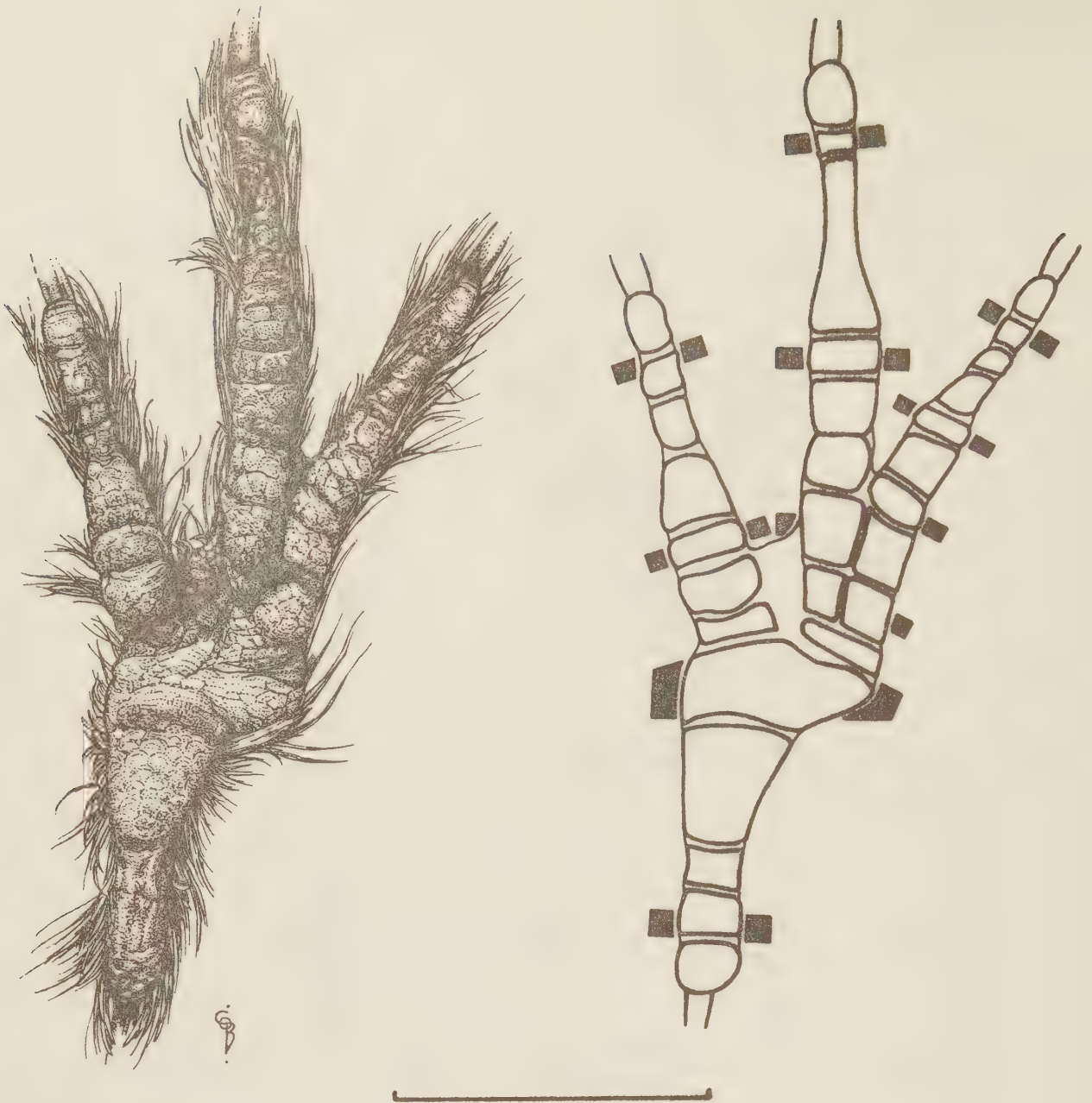


Fig. 11. Pads and folds in (A) Hirundo rustica and (B) Riparia riparia.



HOUSE MARTEN.

Fig. 12. Drawing and diagram of pads and folds in Delichon urbica. Scale indicate 5 mm.

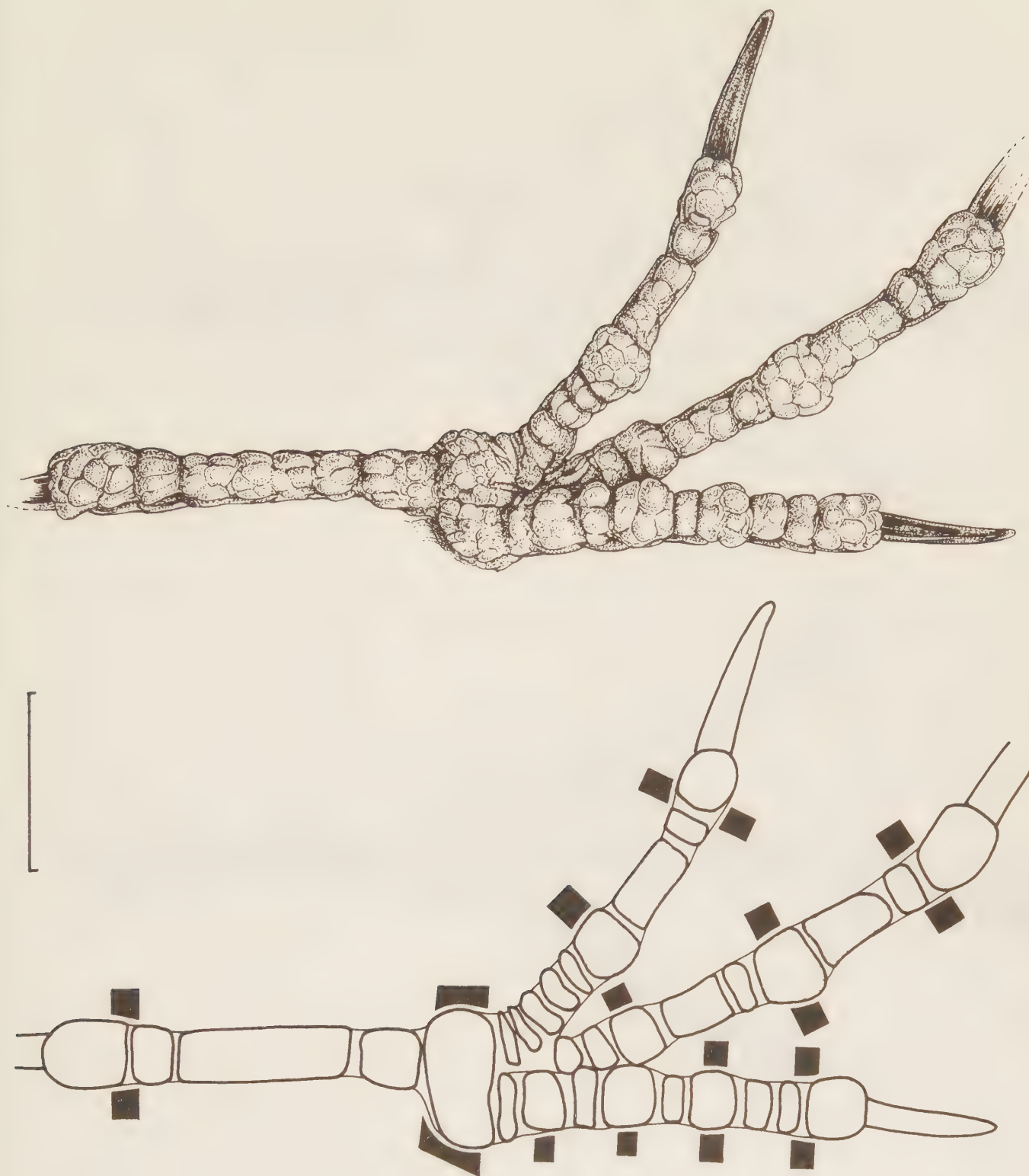


Fig. 13. Drawing and diagram of plantar surface in Alauda arvensis. Scale indicate 5 mm.

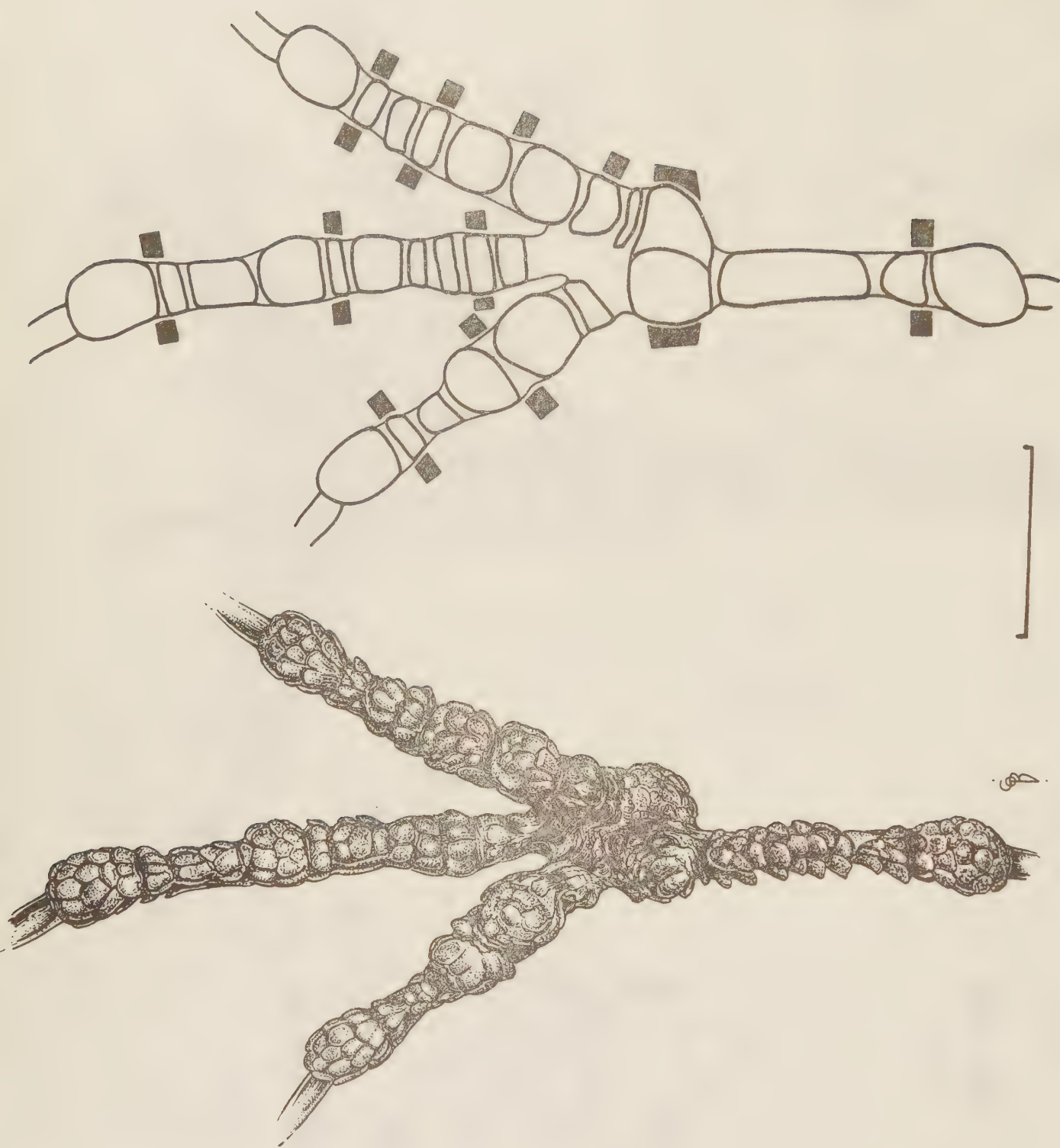


Fig. 14. Drawing and diagram of plantar surface in Plectrophenax nivalis.
Scale indicate 5 mm.

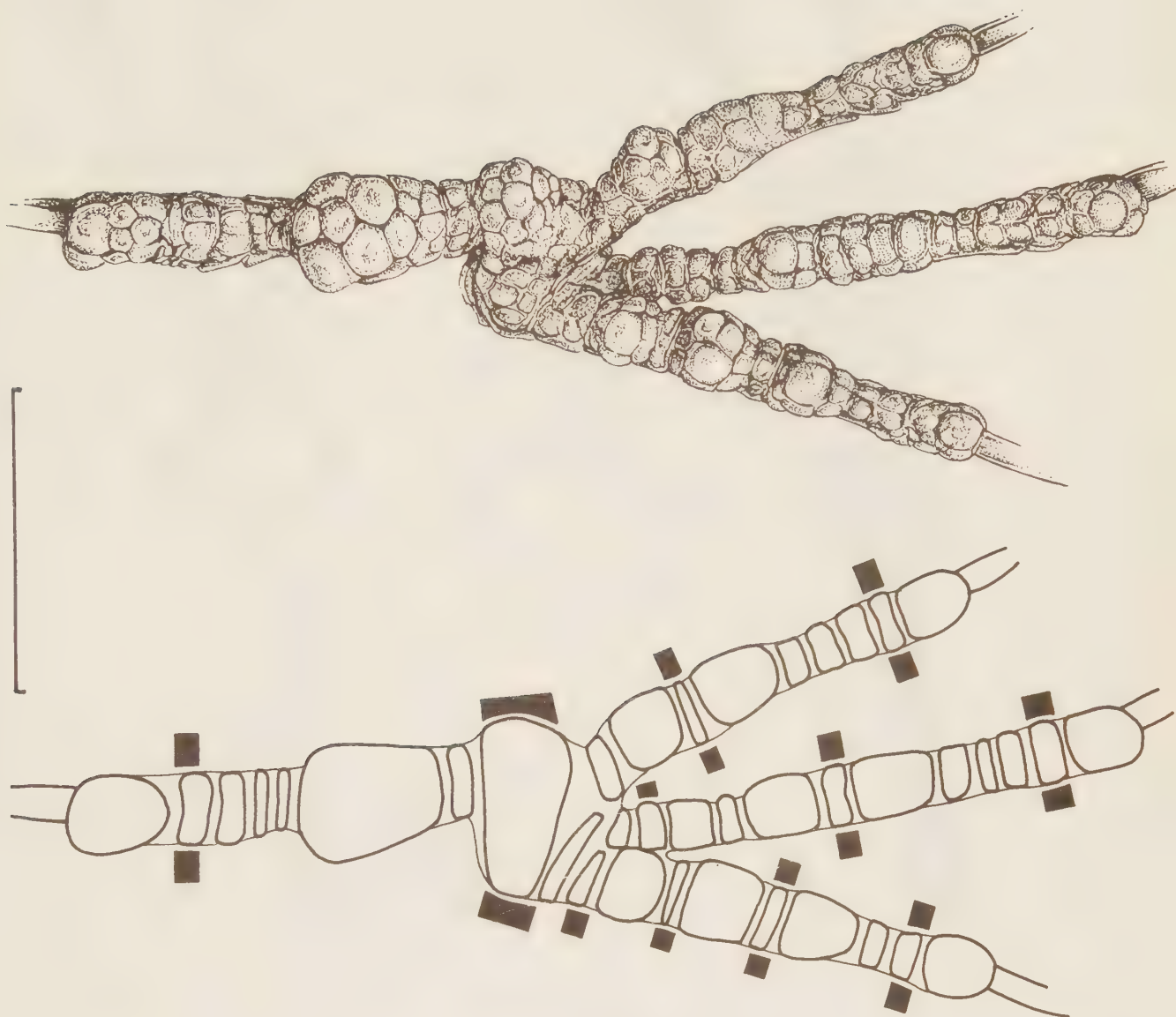
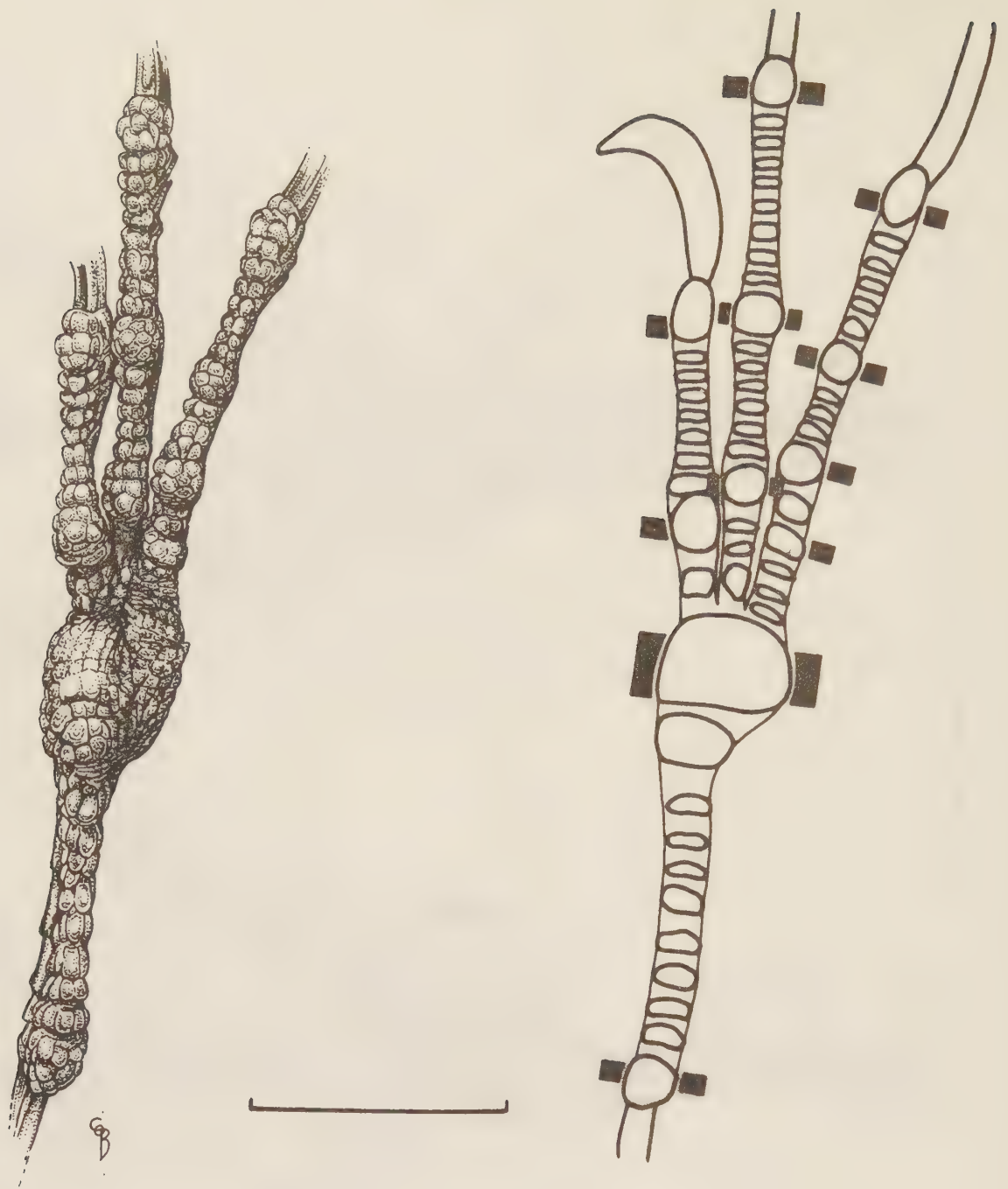


Fig. 15. Drawing and diagram of plantar surface in *Regulus regulus*. Scale indicate 5 mm.



TREE CREEPER.

Fig. 16. Drawing and diagram of plantar surface in Certhia familiaris. Scale indicate 5 mm.

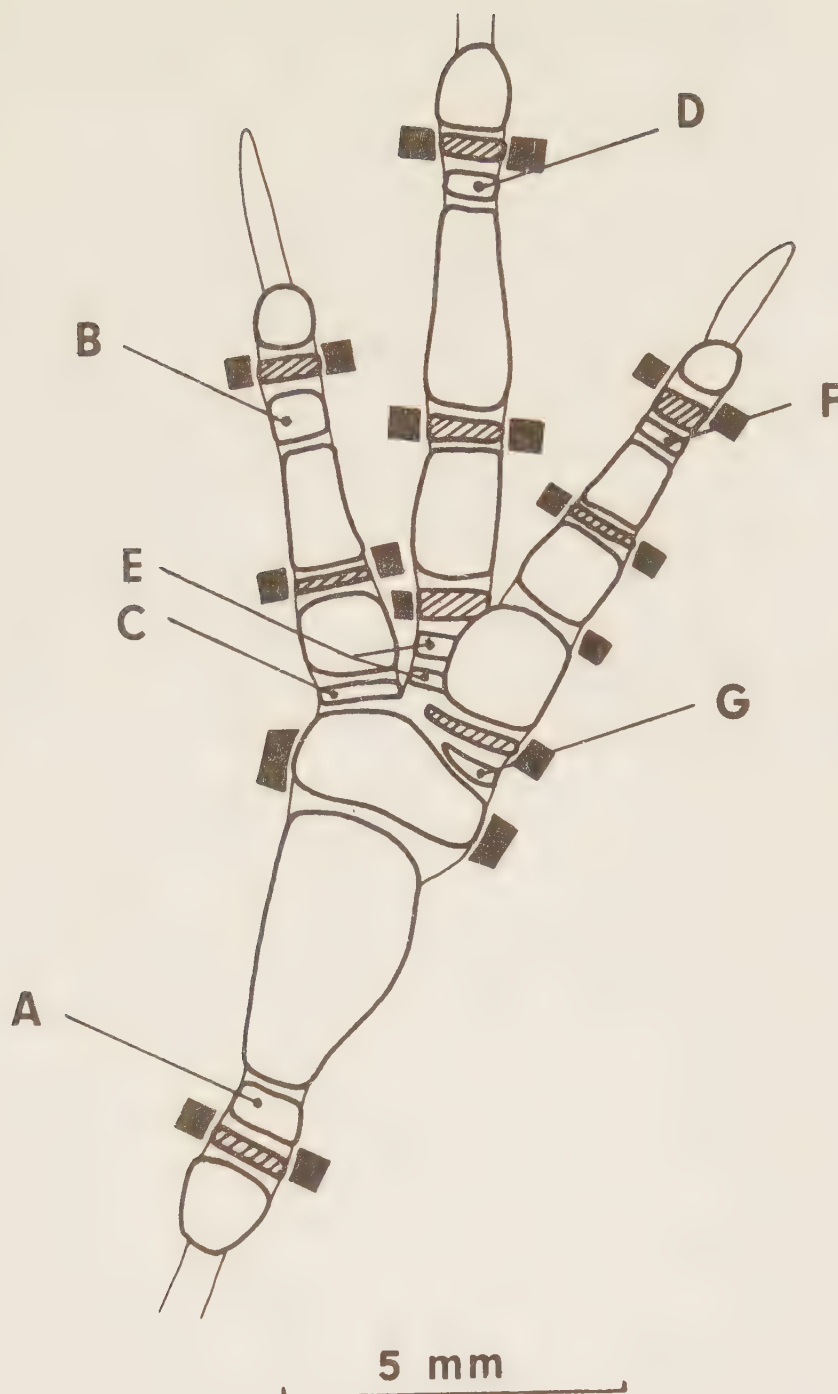


Fig. 17. Pads and folds in Phylloscopus trochilus, the same bird as in Fig. 1. The folds at the joints are shadowed; the folds designated A, B, C, D, E, F, and G are discussed in the text.

IV. Pads and papillae in the feet of nine passerine species.

ABSTRACT

Eight pads in the feet of six warbler species of the genera Sylvia and Phylloscopus and three tit species of the genus Parus were studied. Pad size, number of papillae, papilla size, and phalanx length were calculated. The features are species specific and consequently have a genetic basis. The number of papillae is determined during a short period of embryonic development, but the pads grow successively until the birds leave the nest. The papilla size is determined by an interaction of the growth of pad and the induction of papillae. The comparison of species shows that selection forces act on each of the three features pad size, number of papillae, and papilla size. The differences between P. caeruleus, P. palustris, and P. major are possibly adaptations to different parts of the trees in broad-leaved woods.

CONTENTS

Introduction
Material and methods
Results
Discussion
Literature

INTRODUCTION

The skin in the feet of passerine species consists of pads and folds separated by furrows. The pads are furnished with papillae. The features have been described in an earlier study (p. 21). The present study is a comparison of the size of pads, the number of papillae, the size of papillae, and the length of phalanges in six warbler species of the genera Phylloscopus and Sylvia and three tit species of the genus Parus.

MATERIAL AND METHODS

The species and number of investigated birds are Sylvia curruca (20), Sylvia communis (20), Sylvia atricapilla (16), Sylvia borin (20), Phylloscopus

trochilus (20), Phylloscopus sibilatrix (20), Parus caeruleus (17), Parus palustris (10), and Parus major (20). The warblers were caught during the autumn migration at Ottenby Bird Station, Öland in the Baltic, and the tits in South Sweden.

The feet were fixed in Bouin's mixture or a mixture of 80 per cent alcohol, concentrated formol, and concentrated acetic acid in the proportions 18:1:1. The pads and folds in the third digit of Phylloscopus trochilus were measured before and after fixation and after one month in the fixative, but no length changes due to swelling or shrinking could be recognized.

The way of grasping twigs of different size was studied in one Parus caeruleus and one Parus major, which were kept in a cage.

The pads were studied through a stereo microscope with a camera lucida apparatus. The contour of each pad was drawn on paper of good quality and uniform thickness, and the point of each papilla was marked. The paper was then cut along the drawn outline. The pad size was calculated from the weight of the cut out piece of paper. The papillae were counted, and the papilla size was calculated through the quotient of pad size by number of papillae. In this way, the papilla size is the area occupied by the base of the papilla and is independent of any seasonal changes in the morphology of the papilla (p. 99). The digit was cut sagittally, and the phalanx length was measured from the tubercles of the base to one of the condyles of the head by means of a micrometer scale in the ocular lens of the stereo microscope.

RESULTS

Fig. 1 shows diagrams of pads and folds in Phylloscopus trochilus and Parus major. The designation of pads follows that used in an earlier study (p. 6).

The pads of the claw - pad I:1, II:1, III:1, and IV:1 - have a rounded surface, not suitable for measurements of pads size. The remaining eight pads - pad I:2, II:2, II:3, III:2, III:3, IV:2, IV:3, and IV:4 - have a flat surface and distinct borders; they were examined in the present study.

There is an individual variation in the occurrence of folds. Between pad III:1 and pad III:2 in Phylloscopus trochilus, for instance, there are two folds in most birds, but the proximal fold is lacking in about 40 per cent (p. 24). When there is only one fold, the proximal of the two folds has fused with pad III:2. This individual variation affects the size of pad III:2. To avoid this, the birds with only one fold were treated so that the distal row of papilla in pad III:2 was not included in the calculation of pad size.

Thus all measurements on pad III:2 conformed to the type in Fig. 1 even when there was only one fold between pad III:1 and pad III:2. Similar individual variation occurs at the distal part of pad I:2, II:2, and IV:2; this variation was treated in the same way as that at pad III:2.

Another type of variation occurs at the joints in the middle of the digits. For instance, the fold at joint IV:2/3 is lacking in 5 per cent of Phylloscopus trochilus, and the fold at joint IV:3/4 is lacking in 15 per cent (p. 24). This variation depends on the fold failing to develop during the embryonic life. It is not known how much this variation affects the size of the pads.

All warblers, irrespective of species, were measured as if the pattern of pads and folds conformed to that in Fig. 1A, and all the tits, to that in Fig. 1B.

Thus, eight pads and eight phalanges were studied in each bird. Tables 1-8 show the mean values and standard deviations for the species. Analysis of variance was performed and the significances between means of the most similar species are indicated in the tables. Table 9 gives a compilation of the total size of pads, total number of papillae, mean papilla size and total phalanx length.

The papilla size can be compared both in the pads within species and in the pads of different species. Consequently, the papilla size was studied by analysis of variance in a split-plot design. The animals are the main plots and the eight pads the subplots. The five components of variance are species, pads, species x pads (interaction), animals within species, and error. Table 9 records the result of the analysis.

In the following, the most closely related species are compared.

Sylvia curruca - Sylvia communis

S. curruca is a smaller species than S. communis. It weighs on average 11,5 g compared with 13 g; it has shorter tarsi, bill, wing, and tail (information in various handbooks). All phalanges of S. curruca are shorter than corresponding phalanges of S. communis (Tables 4, 9). This difference between the species also appears in the sole: six pads are smaller and two pads have fewer papillae in S. curruca (Tables 1, 2). The difference is most pronounced in the papilla size: in all pads, S. curruca has smaller papillae than S. communis (Table 3). The differences in papilla size are greater in the pads of digit II and less in the pads of digit IV ($P < 0.05$ for interaction, Table 10).

Sylvia atricapilla - Sylvia borin

These two species both weigh about 17 g. The feet are the same size, and there is no difference between the length of phalanges (Table 4). All pads are of equal size, but the number of papillae differ in four pads (Tables 1, 2). The papilla size differs significantly only in two pads (Table 3), but all calculated means in S. atricapilla are bigger than those of S. borin; this difference between the two species is significant (Tables 9, 10).

Phylloscopus trochilus - Phylloscopus sibilatrix

Both species weigh about 9 g. The phalanges are of equal length (Table 4). Ph. sibilatrix has seven pads larger and six pads with more papillae than Ph. trochilus (Tables 1, 2). But the papilla size differs only in three pads, the difference being rather slight (Table 3, 10).

Parus caeruleus - Parus palustris - Parus major

Two species, P. caeruleus and P. palustris, both weigh about 11 g; P. major weighs about 19 g. The total length of eight phalanges shows that P. palustris is intermediate between P. caeruleus and P. major (Table 9), but digit III and digit IV of P. palustris are about the same length as those of P. caeruleus (Table 8).

The total figures of pad size and the mean values of papilla size (Table 9) show that P. palustris is intermediate between P. caeruleus and P. major, but in respect of papilla number, P. palustris has less papillae than the other species. This is an overall picture; the relation in the different pads is more complicated.

First, the sole of P. palustris and that of P. caeruleus are compared. Seven pads of P. palustris are larger than the corresponding pads of P. caeruleus (Table 5); six pads have less papillae (Table 6). All pads of P. palustris have larger papillae than the corresponding pads of P. caeruleus (Table 7).

Next, the sole of P. major and that of P. palustris are compared. Four pads of P. major are larger and one pad smaller than the corresponding pads of P. palustris (Table 5). The number of papillae differs in four pads (Table 6). The papilla size is similar in the two proximal pads of digit II and digit IV: pad II:2, II:3, IV:3, and IV:4; in the remaining pads, P. major has larger papillae (Table 7).

In P. caeruleus, the papilla size ranges from 0.079 to 0.109 mm²; in P. palustris, from 0.126 to 0.158 mm²; and in P. major, from 0.115 to 0.179 mm² (Table 7). If the small papillae in pad IV:2 of P. caeruleus are disregarded, the remaining pads in this species have about the same papilla size. The greatest range of variation in papilla size occurs in P. major, where pad I:2

and pad III:2 have notably large papillae.

P. caeruleus feeds high up in the trees, often hanging upside-down. As observed in cage birds, all eight pads are involved in the grasp of thin twigs. P. major has larger feet and a greater range of variation in papilla size. It has another way of grasping thin twigs; it pinches the twig between the proximal part of digit II and digit IV above the twig and the proximal part of digit I below. Pad II:2, II:3, IV:3, IV:4, and proximal part of pad I:2 are involved in this grasp. P. major uses pad III:2 and most of the surface of pad I:2 on thicker twigs. The mentioned pads in digit II and digit IV have smaller papillae than the pads in digit I and digit III. This indicates that the smaller papillae are adapted to grasp fine twigs.

The grasp of P. palustris was not studied in living birds, but it is notable that pad II:2, II:3, IV:3, and IV:4 in P. palustris have the same papilla size as corresponding pads in P. major.

DISCUSSION

Pad size, number of papillae, papilla size, and phalanx length in the closely related species were compared pad by pad. Sylvia atricapilla and S. borin are the most similar species. In the individual birds, it is impossible to determine the species by features in the pads even if the specimens are compared together. But analysis of variance showed that certain mean values in the two species differ significantly. In Phylloscopus trochilus and Ph. sibilatrix, the species can be determined by the features in pad I:2, II:2, III:2, III:3, and IV:4. Sylvia curruca and S. communis can be distinguished by size of pad II:2, II:3, and III:3, and by the notably smaller papillae in many pads of S. curruca.

Besides the species described in the present study, I measured pads and papillae in 28 passerine species, common in south Sweden. All these species could be determined by means of features in the pads and papillae. It is therefore concluded that the features are species specific and that they have a genetic basis.

The development of pads and papillae has been studied in the chick embryo (p. 6). The first morphological sign of a pad is a protuberance of skin which proximally and distally is delimited by deepenings, the embryonic furrows. About two days later, the first papillae develop in the middle of the pad; later, new papillae are added peripherally to the first. After about two days, the entire pad is covered with papillae. The pad grows larger during the

following embryonic life, and the growth continues after hatching. In the nestlings of passerine species, the feet grow until the birds leave the nest. The growth of pad is thus extended over a long period, whereas the number of papillae is determined during a short period of embryonic life. The differences between species clearly show that both the pad size and the number of papillae are subjected to selection forces.

The size of papillae is determined by the interaction of the embryonic processes for growth of pad and for induction of papillae. In the adult bird, the papilla size is calculated by the quotient of pad size and number of papillae. The examined species give evidence that also the papilla size is subjected to selection forces. (i) Phylloscopus trochilus and Ph. sibilatrix have four pads that differ both in pad size and in number of papillae, but have similar papilla size. (ii) Sylvia curruca has all pads with papillae smaller than S. communis; in pad II:2, II:3, and III:3, this is achieved by a difference in pad size with a similar number of papillae, but in pad III:2 by a difference in number of papilla with a similar pad size.

The three Parus species usually coexist in the European broad-leaved woods; in the winter, they feed together in mixed flocks. In English oak woods, the three tit species are ecologically segregated by the food items taken (Lack 1944, 1971, Gibb 1954, Betts 1955). P. major feeds mainly low down, P. palustris at intermediate height, and P. caeruleus in the canopy, and they take mainly larger, intermediate, and smaller insects, respectively. These differences are most pronounced in winter when food is scarce. In Swedish beech woods, the same three species are similarly segregated (Ulfstrand 1962). In the shrub vegetation, they occur together, but differ how they examine the vegetation for food. The beak is adapted to these differences (Snow 1954, Lack 1971). The present study shows that the pads, papillae, and phalanges constitute a second set of features that differ between the three species, being adapted to the substrate in different parts of the habitat. It may be supposed that it is the diameter of the twig and the structure of the bark surface that is important for the adaptation of the papilla size.

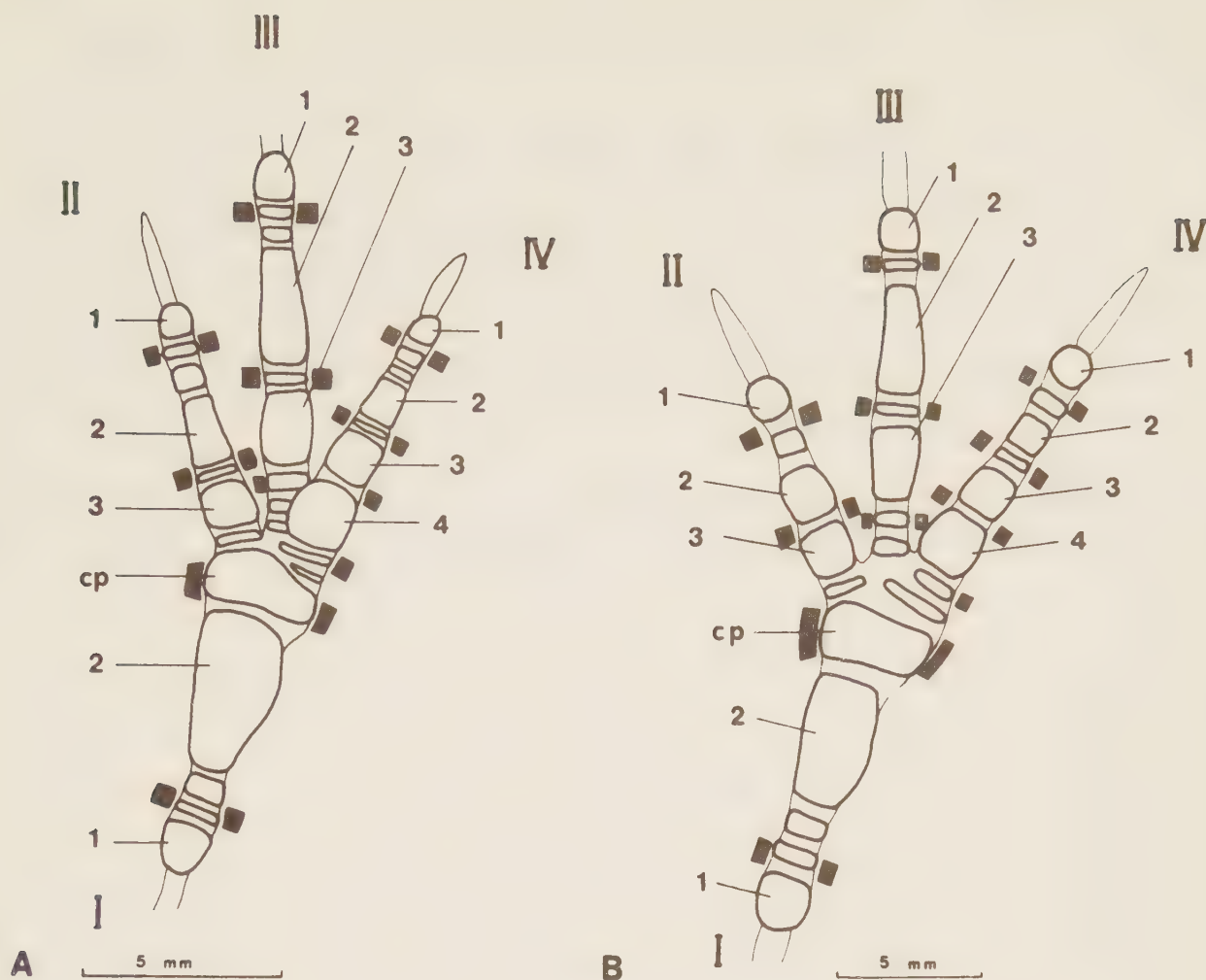


Fig. 1. Diagram of pads and folds in (A) *Phylloscopus trochilus* and (B) *Parus major*. Digits are designated by Roman numerals and pads by Arabic numerals; cp, central pad.

LITERATURE

- Betts, M.M. 1955. The food of Titmice in oak woodland. - J. Anim. Ecol. 24, 282-323
- Gibb, J. 1954. Feeding ecology of tits, with notes on Treecreeper and Goldcrest. - Ibis 96; 513-543.
- Lack, D. 1944. Ecological aspects of species-formation in passerine birds. - Ibis 86, 260-286.
- Lack, D. 1971. Ecological isolation in birds. Blackwell, Oxford & Edinburgh.
- Snow, D.W. 1954. The habitats of Eurasian tits (Parus spp.). - Ibis 96, 565-585.
- Ulfstrand, S. 1962. On the nonbreeding ecology and migratory movements of the Great Tit (Parus major) and the Blue Tit (Parus caeruleus) in southern Sweden. - Vår Fågelvärld, Suppl. 3, 1-145.

Table 1. Pad sizes (mm²) in the Sylvia and Phylloscopus species, shown by mean value - standard deviation. Significance level, SL, indicated between certain means: - for P>0.05, X for P<0.05, XX for P < 0.01, XXX for P<0.001.

Pad	<u>Sylvia</u>			<u>Phylloscopus</u>					
	<u>curruca</u>	<u>SL</u>	<u>communis</u>	<u>atricapilla</u>	<u>SL</u>	<u>borin</u>	<u>trochilus</u>	<u>SL</u>	<u>sibilatrix</u>
I:2	8.27-0.84	*	8.79-0.78	10.01-0.83	-	10.05-0.81	5.82-0.45	***	6.52-0.77
II:2	1.96-0.16	***	2.42-0.23	2.41-0.31	-	2.47-0.23	1.44-0.18	***	1.70-0.17
II:3	1.90-0.23	***	2.23-0.35	2.50-0.28	-	2.48-0.38	1.20-0.11	-	1.28-0.16
III:2	3.61-0.27	-	3.69-0.51	3.91-0.44	-	3.84-0.52	2.47-0.26	***	2.84-0.31
III:3	2.65-0.36	***	3.27-0.38	3.47-0.31	-	3.34-0.52	1.91-0.23	***	2.28-0.23
IV:2	1.08-0.23	-	1.16-0.18	1.26-0.16	-	1.16-0.20	0.73-0.15	*	0.83-0.13
IV:3	1.71-0.14	***	1.98-0.16	2.18-0.22	-	2.13-0.22	1.26-0.16	**	1.46-0.13
IV:4	2.61-0.42	*	3.08-0.67	3.74-0.66	-	3.49-0.52	1.86-0.25	***	2.41-0.31

Table 2. Number of papillae in the Sylvia and Phylloscopus species, shown by mean value - standard deviation. Significance level, SL, indicated between certain means: - for $P > 0.05$, X for $P < 0.05$, XX for $P < 0.01$, XXX for $P < 0.001$.

Pad	<u>Sylvia</u>			<u>Phylloscopus</u>					
	<u>curruca</u>	<u>SL</u>	<u>communis</u>	<u>atricapilla</u>	<u>SL</u>	<u>borin</u>	<u>trochilus</u>	<u>SL</u>	<u>sibilatrix</u>
I:2	137-17	*	126-18	176-20	**	195-19	112-9	***	125-9
II:2	39-5	-	38-6	47-7	*	53-9	31-5	***	40-4
II:3	37-7	-	35-5	47-7	*	53-10	22-4	**	28-5
III:2	60-6	**	52-9	72-11	-	77-13	45-6	***	56-6
III:3	46-8	-	48-7	63-9	-	67-11	36-6	***	43-7
IV:2	26-6	-	25-7	32-7	-	32-9	21-4	-	22-5
IV:3	37-5	-	38-5	49-7	**	55-12	31-4	-	36-6
IV:4	53-9		54-11	72-14	-	76-15	36-6	**	49-10

Table 3. Papilla sizes (mm²) in the Sylvia and Phylloscopus species, shown by mean value - standard deviation. Significance level, SL, indicated between certain means: - for P > 0.05, X for P < 0.05, XX for P < 0.01, XXX for P < 0.001.

Pad	<u>Sylvia</u>			<u>Phylloscopus</u>		
	<u>curruca</u>	<u>SL</u>	<u>communis</u>	<u>atricapilla</u>	<u>SL</u>	<u>trochilus</u> <u>SL</u> <u>sibilatrix</u>
I:2	0.062-0.010	***	0.071-0.013	0.058-0.007	*	0.052-0.004 - 0.052-0.005
II:2	0.052-0.008	***	0.065-0.010	0.053-0.009	-	0.048-0.008 * 0.043-0.004
II:3	0.052-0.008	***	0.064-0.011	0.054-0.009	*	0.055-0.010 ** 0.047-0.008
III:2	0.061-0.008	**	0.072-0.013	0.054-0.007	-	0.055-0.009 * 0.051-0.006
III:3	0.059-0.013	**	0.069-0.008	0.056-0.008	-	0.055-0.009 - 0.054-0.007
IV:2	0.042-0.006	*	0.047-0.008	0.041-0.007	-	0.036-0.004 - 0.038-0.005
IV:3	0.047-0.007	**	0.052-0.005	0.045-0.005	-	0.042-0.002 - 0.043-0.011
IV:4	0.050-0.005	**	0.058-0.011	0.053-0.008	-	0.052-0.005 - 0.050-0.006

Table 4. Phalanx lengths (mm) in the Sylvia and Phylloscopus species, shown by mean value - standard deviation. Significance level, SL, indicated between certain means: - for $P > 0.05$, X for $P < 0.05$, XX for $P < 0.01$, XXX for $P < 0.001$.

Pad	<u>Sylvia</u>			<u>Phylloscopus</u>					
	<u>curruca</u>	<u>SL</u>	<u>communis</u>	<u>atricapilla</u>	<u>SL</u>	<u>borin</u>	<u>trochilus</u>	<u>SL</u>	<u>sibilatrix</u>
I:2	6.72-0.20	***	7.21-0.22	7.42-0.22	-	7.55-0.25	6.06-0.19	-	6.26-0.18
II:2	3.52-0.23	***	4.07-0.24	3.78-0.90	-	4.31-0.27	3.39-0.29	-	3.52-0.22
II:3	2.71-0.20	***	3.30-0.24	3.29-0.30	-	3.26-0.27	2.70-0.18	-	2.57-0.10
III:2	4.28-0.47	***	4.86-0.30	5.03-0.45	-	5.08-0.34	4.12-0.19	-	4.01-0.24
III:3	3.46-0.45	***	4.02-0.53	3.97-0.49	-	3.87-0.27	3.05-0.17	-	3.16-0.23
IV:2	2.20-0.27	***	2.52-0.37	2.78-0.21	-	2.86-0.24	2.17-0.16	*	2.28-0.11
IV:3	1.82-0.13	***	2.04-0.18	2.17-0.21	-	2.25-0.48	1.67-0.12	-	1.71-0.16
IV:4	1.90-0.24	***	2.27-0.38	2.19-0.23	-	2.14-0.25	1.65-0.14	-	1.72-0.22

Table 5. Pad sizes (mm^2) in the Parus species, shown by mean value-standard deviation. Significance level, SL, indicated between certain means: - for $P > 0.05$, X for $P < 0.05$, XX for $P < 0.01$, XXX for $P < 0.001$.

Pad	<u>Parus</u>				
	<u>caeruleus</u>	<u>SL</u>	<u>palustris</u>	<u>SL</u>	<u>major</u>
I:2	7.35-0.60	***	7.67-0.50	***	9.92-1.12
II:2	2.03-0.16	***	2.91-0.23	***	2.77-0.28
II:3	1.99-0.15	***	2.90-0.35	-	3.04-0.32
III:2	2.53-0.29	***	2.87-0.28	***	3.70-0.39
III:3	2.14-0.20	***	2.95-0.23	-	3.10-0.37
IV:2	1.03-0.12	***	1.29-0.19	-	1.31-0.17
IV:3	1.93-0.18	***	2.12-0.16	***	2.40-0.20
IV:4	2.15-0.18	-	2.20-0.17	***	2.90-0.32

Table 6. Number of papillae in the Parus species, shown by mean value-standard deviation. Significance level, SL, indicated between certain means: - for $P > 0.05$, X for $P < 0.05$, XX for $P < 0.01$, XXX for $P < 0.001$.

Pad	<u>Parus</u>				
	<u>caeruleus</u>	<u>SL</u>	<u>palustris</u>	<u>SL</u>	<u>major</u>
I:2	68-5	***	56-4	-	56-8
II:2	22-2	**	20-3	-	19-2
II:3	19-2	*	20-2	-	21-3
III:2	26-3	***	18-2	**	21-4
III:3	22-3	*	21-1	-	20-4
IV:2	13-2	***	10-1	***	12-2
IV:3	21-2	***	17-1	***	20-3
IV:4	24-3	***	17-2	***	23-3

Table 7. Papilla sizes (mm²) in the Parus species, shown by mean value-standard deviation. Significance level, SL, indicated between certain means: - for P > 0.05, X for P < 0.05, XX for P < 0.01, XXX for P < 0.001.

Pad	<u>Parus</u>				
	<u>caeruleus</u>	<u>SL</u>	<u>palustris</u>	<u>SL</u>	<u>major</u>
I:2	0.109-0.008	***	0.136-0.010	***	0.179-0.021
II:2	0.094-0.008	***	0.145-0.020	-	0.148-0.022
II:3	0.105-0.012	***	0.145-0.019	-	0.148-0.017
III:2	0.099-0.009	***	0.158-0.012	***	0.177-0.028
III:3	0.098-0.013	***	0.140-0.009	***	0.156-0.023
IV:2	0.079-0.012	***	0.130-0.014	***	0.115-0.021
IV:3	0.091-0.011	***	0.126-0.009	-	0.122-0.017
IV:4	0.092-0.011	***	0.129-0.011	-	0.127-0.021

Table 8. Phalanx lengths in the Parus species, shown by mean value-standard deviation. Significance level, SL, indicated between certain means: - for P > 0.05, X for P < 0.05, XX for p < 0.01, XXX for P < 0.001.

Pad	<u>Parus</u>				
	<u>caeruleus</u>	<u>SL</u>	<u>palustris</u>	<u>SL</u>	<u>major</u>
I:2	6.75-0.19	***	6.92-0.18	***	7.78-0.18
II:2	3.41-0.43	***	3.66-0.15	***	3.93-0.16
II:3	2.93-0.37	***	3.84-0.24	-	3.93-0.26
III:2	4.18-0.21	-	4.22-0.16	***	5.02-0.26
III:3	3.06-0.34	*	3.28-0.16	***	3.61-0.25
IV:2	2.75-0.28	-	2.62-0.18	***	2.96-0.25
IV:3	1.99-0.17	*	2.12-0.12	***	2.34-0.17
IV:4	1.88-0.11	-	1.95-0.10	***	2.22-0.23

Table 9. Measures of pads, papillae, and phalanges in Sylvia, Phylloscopus, and Parus species.

Species	Total pad size mm ²	Total papilla number	Mean papilla size mm ²	Total phalanx length mm
<u>S. curruca</u>	23.8	433	0.053	26.6
<u>S. communis</u>	26.6	415	0.062	30.4
<u>S. atricapilla</u>	29.5	559	0.052	31.1
<u>S. borin</u>	29.0	608	0.047	31.3
<u>Ph. trochilus</u>	16.7	334	0.049	24.8
<u>Ph. sibilatrix</u>	19.3	399	0.047	25.2
<u>P. caeruleus</u>	21.2	214	0.096	27.0
<u>P. palustris</u>	24.9	179	0.139	28.6
<u>P. major</u>	26.2	192	0.147	31.8

Note. Values are calculated from the mean in Tables 1 - 8. Pad size and number of papillae are total of eight pads; papilla size, mean of eight pads; phalanx length, total of eight phalanges.

Table 10. Significances derived by analysis of variance on papilla size.

Species investigated	Variance ratio			
	<u>animal</u> error	<u>pad</u> error	<u>species</u> <u>animal</u>	<u>species x pad</u> error
<u>Sylvia</u> spp.	xxx	xxx	xxx	xxx
<u>S. curruca</u> + <u>S. communis</u>	xxx	xxx	xxx	x
<u>S. atricapilla</u> + <u>S. borin</u>	xxx	xxx	x	0
<u>Phylloscopus</u> spp.	xxx	xxx	0	xxx
<u>Parus</u> spp.	xxx	xxx	xxx	xxx

Note. Level of significance indicated by 0: $P > 0.05$, X: $P < 0.05$,
 XX: $P < 0.01$, XXX: $P < 0.001$

V. Pads and folds in species with zygodactyle feet.

ABSTRACT

A comparative study of pads and folds is made on the zygodactyle feet of three species of woodpecker, one species of cuckoo, and three species of parrot.

The pads are related to either the phalanges or the joints. Woodpeckers have one pad at each of the phalanges in the four digits and one pad at each of the proximal joints of the anterior digits. Cuckoos have one pad at each of the phalanges and one fold at certain joints, including the proximal joints of the anterior digits - the latter feature being fundamentally different from the woodpeckers. Parrots have all pads about the same size, and there is no fold at any of the joints. There is one pad at each of the ultimate and penultimate phalanges, but the remaining pads in the digits are interpreted as joint pads that are subdivided in the anterior digits. The pattern of pads in the parrots has no counterpart in any other bird order, indicating a separate evolution of the foot in the parrots.

CONTENTS

Introduction

Material and methods

Species

Picus viridis

Jynx torquilla

Cuculus canorus

Aratinga aurea

Discussion

Literature

INTRODUCTION

The woodpeckers of the family Picidae, the cuckoos of the family Cuculidae, and the parrots of the family Psittacidae have the fourth digit permanently directed posteriorly in a zygodactyle or yoke-shaped arrangement. There is little published information on the pattern of pads and folds in birds with

zygodactyle feet (Bock & Miller 1959), and the aim of the present study is to describe and compare these structures in some species representative of the three families. The attachment of the pads to the skeletal elements in the parrot is described in a separate study (p. 62).

The zygodactyle foot is suitable for perching on twigs (Bock & Miller 1959). This perching habit is normal in cuckoos and parrots. The first and second digits are relatively short and suitable for grasping thin twigs, whereas the third and fourth digits are long and suitable for grasping thick twigs. Many woodpeckers, however, climb on tree trunks; therefore the zygodactyle foot of woodpeckers has been characterized as a scansorial foot.

Linné interpreted the zygodactyle foot as a climbing foot. In the tenth edition of *Systema Naturae* (1758), the order Picae comprised three groups of genera; one of these was diagnosed by pedibus scansorius, or two anterior and two posterior digits. During the nineteenth century, many authors used the terms Scansores, Zygodactyli, or Fibulatores in the classification of birds with such feet.

The woodpeckers show particular adaptive modifications in the leg skeleton, leg muscles, and tail for tree-trunk climbing, which supports the opinion that the zygodactyle foot is not primarily a climbing foot (Burt 1930, Scharnke 1930, Stolpe 1932, Richardson 1942). Bock & Miller (1959) recognized two different lines of climbing modification in the feet of woodpeckers. In the short-hallux line, the first digit can rotate and adopt a postero-lateral direction; the fourth digit is longer than the third and can also be rotated laterally. This adaptation occurs in the genera Picus and Dendrocopos, used in the present study, although the two genera are probably not closely related (Goodge 1972). In the long-hallux line, the first digit has lost all connexions with the second digit and the first digit has moved laterally or even antero-laterally. The most extreme adaptation on this line occurs in the ivory-billed woodpeckers, genus Phloecestes. The feet on the short-hallux line and on the long-hallux line must be regarded as independently acquired modifications for climbing within the family Picidae (Bock & Miller 1959).

MATERIAL, METHODS, AND TERMINOLOGY

The feet of the following species (the number of birds is indicated in brackets) were studied in fresh or fixed condition.

Family Picidae: Jynx troquilla (1), Picus viridis (2), Dendrocopos major (5).
Family Cuculidae: Cuculus canorus (5). Family Psittacidae: Aratinga aurea

(a parakeet) (1), Poicephalus robustus (a parrot) (1), Melopsittacus undulatus (2).

This material was complemented by study skins in the zoological museum at the university of Lund and in the museum of natural history in Gothenburg. The skins involve fourteen species of parrots, including Nestor notabilis and Strigops habroptilus. The woodpeckers and cuckoos comprise several specimens of the common Scandinavian species. In the dried feet, the large pads are easily recognized, but it is often impossible to determine the small folds and some of the furrows; therefore the following description is mainly based on the observations of fresh or fixed material.

The pads and folds were pictured in diagrams (Fig. 1-2). Their position in the plantar surface was determined in relation to the phalanges or joints, which were localized after dissection of the digits.

The pads and folds are designated according to the adjacent phalanx or joint. The designation is described in an earlier study (p. 6).

A furrow is determined when the papillae in the plantar surface are separated by a gap which opens and closes when the digit is bent and straightened.

The large structures in plantar skin are pads, and the small structures are folds. Certain folds are small and lack papillae. Other folds have papillae that deviate from those in the pads, and this seems to depend on their not being worn against the substrate. Still other folds have papillae similar to those in the pads. It is therefore impossible to distinguish clearly between pads and folds.

SPECIES

Picus viridis (Fig. 1A)

The first digit is short, and the anterior digits are joined by skin and connective tissue in the region of phalanx II:3 and phalanx III:4.

Pad II:2/3 and pad III:3 have fused to one big elevated pad, supported by a large amount of connective tissue. Pad II:3 and pad III:4 have also fused, but this is smaller with little subcutaneous tissue. The principle function of grasping or resting on the substrate is exerted by the central pad and pad II:2/3 + III:3/4, whereas the interjacent pad II:3 + III:4 has a function comparable to a fold (cf. Fig. 3, Chapter II).

There is a fold at joint III:3/4, but this is missing in one of the examined birds, indicating an individual variation comparable to that observed in passerine species (p. 21). Pad III:3 is subdivided into two pads, the distal pad

being large and elevated.

The fourth digit has one pad at each of the five phalanges, but no fold at any of the joints.

Pad II:2 and pad III:2 are subdivided.

Jynx torquilla (Fig. 1B)

The feet of Jynx torquilla are smaller than those of Picus viridis, and the digits are more slender. The anterior digits are free from each other.

Pad II:2/3 is free from pad III:3/4. The central pad is subdivided by a longitudinal furrow into two pads, one at the base of the first digit and the other at the base of the fourth digit. Pad II:3 and pad III:4 have fused.

The first digit has a narrow pad I:2; distal to this there are two folds. The proximal of the two folds is interpreted as a separated part of pad I:2.

The second digit has pad II:2 subdivided. The proximal of the two folds at the distal joint is interpreted as a separated part of pad II:2.

The third digit has pad III:3 subdivided into two pads. There is a fold at joint III:2/3.

The fourth digit has one pad at each of the five phalanges and one fold at the distal joint.

Cuculus canorus (Fig. 2A)

The anterior digits are connected at phalanx II:3 and phalanx III:3. Pad II:3 and pad III:4 have fused to one large pad, separated from the central pad by a wide furrow, which functions as a hinge between the anterior and the posterior digits.

The most distinctive feature in Cuculus canorus is that the phalanx pads are well developed, and that there is one pad at each of the fourteen phalanges.

Pad III:2 is subdivided.

There is one fold at each of the seven joints, but the folds are small and some of them lack papillae. The small folds are probably lacking in certain individuals.

Aratinga aurea (Fig. 2B)

The pads in Aratinga aurea differ basically from those in the other species. All the pads are about the same size, and it is notable that there is no fold at any of the joints.

The attachment of the pads to the skeletal elements is described in a separate study (p. 68).

The fourth digit has five pads. The two distal pads are related to the phalanges, whereas the three proximal pads are related to the joints, although they are somewhat displaced in relation to the joints. The furrow between pad IV:5 and the central pad lies in the central foot, ventral to tarsometatarsus.

In the second digit, the two proximal pads are attached to joint II:2/3 and are interpreted as a subdivided joint pad, pad II:2/3.

In the third digit, two pads are attached to joint III:2/3 and are interpreted as a subdivided joint pad. The two proximal pads are attached to joint III:3/4 and are also a subdivided joint pad.

The first digit has three pads. The middle pad is smaller and is attached to phalanx I:2. The proximal pad is attached to phalanx I:2 and tarsometatarsus. The furrow between proximal pad I:2 and central pad lies ventral to metatarsus I.

DISCUSSION

The woodpeckers of the family Picidae consist of 213 species (Storer 1971). Many of them show adaptive modifications in the foot, skeleton, and muscles for tree trunk climbing (references in 'Introduction'). Jynx torquilla is a medium-sized species, classified in the subfamily Jynginae by Vaurie (1965). It is regarded as an ancestral type of woodpecker (Steinbacher 1964, Bock & Miller 1959, Goodge 1972). It does not climb on tree trunks.

Dendrocopos major has smaller feet and shorter digits than Picus viridis. The pattern of pads and folds in the two species is similar in most respects, but deviates in that pad I:2, II:2, III:2, and IV:2 in Dendrocopos major are subdivided into two, three, or four folds. A similar subdivision of the mentioned pads occurs in Dendrocopos minor and Picoides tridactylus.

Jynx torquilla has the anterior digits free, whereas Picus viridis and Dendrocopos major have the basal phalanges joined by connective tissue and skin. Connexion of the basal phalanges in the anterior digits also occurs in jacamars, puffbirds, barbets, and toucans, which are classified in the suborder Galbulae of the order Piciformes, but these birds do not climb on tree trunks. The connexion of the anterior digits is therefore not an adaptation for tree trunk climbing (cf. Richardson 1942); instead, a co-ordination and enforcement of the grasping of the substrate.

Picus viridis and Dendrocopos major have pad II:2/3 and pad III:3/4 fused to one large pad. Jynx torquilla has the corresponding pads free from each other.

The difference between Jynx torquilla and the other woodpeckers, in the connexion of the anterior digits and the morphology of pad II:2/3 and pad III:3/4, indicates that Jynx torquilla is less specialized than the other woodpeckers.

The cuckoos of the family Cuculidae number 130 species (Storer 1971). They are mainly arboreal, although some are secondarily adapted for rapid running on the ground. Only one species of cuckoo was studied, the Cuculus canorus in the subfamily Cuculinae (Vaurie 1965). It is a medium-sized species and shows no particular specializations. It lives in trees and bushes, where it takes most of its food.

Pad II:3 and pad III:4 in Cuculus canorus have fused to one large pad. There is one fold at each of joint II:2/3 and joint III:3/4.

The large pad II:3 + III:4 in Cuculus canorus corresponds to a comparatively small pad in the woodpeckers, whereas the folds at joint II:2/3 and joint III:3/4 correspond to a fused and large pad in the woodpeckers.

A large pad at a joint impedes the bending of the digit in that joint. Therefore, the occurrence of pads at joint II:2/3 and joint III:3/4 in the woodpeckers but folds at these joints in the Cuculus canorus is fundamental and indicates different functions in the proximal parts of the anterior digits.

The parrots in family Psittacidae are large in number, 339 species (Storer 1971). They deviate in morphology, food, and habits from other birds, and the order is clearly delimited (Dorst 1964). Many parrots climb in trees by means of the feet with the co-operation of the beak. The foot is also used to grasp things and convey them to the beak.

The parrot Poicephalus robustus has exactly the same pattern of pads as Aratinga aurea; it differs only in one minor respect; namely, that there are two folds between pad I:1 and pad I:2. This means that the pattern in the first digit is comparable to that in the passerine species (p. 21), although pad I:2 has a different attachment to the skeletal elements (p. 62); the remaining three digits have the ordinary parrot pattern. Melopsittacus undulatus is a small species and probably frequents small branches as most passerine species. It is therefore notable that the pattern of pads shows almost no convergence to that in the Passeriformes (p. 21).

The analysis of the pads in the parrots also includes the attachment of the pads to the skeletal elements (p. 62). According to the attachment, the two proximal pads in the second digit are interpreted as a subdivided joint pad. The four proximal pads in the third digit are similarly interpreted as two subdivided joint pads. The three proximal pads in the fourth digit are undivided joint pads. There are no phalanx pads at these phalanges. The interpretation

of the pads as joint pads and not as phalanx pads is supported by the fact that between the pads there is no fold that could be interpreted as a reduced joint pad, as is the case in Cuculus canorus or in the passerine species (p. 35).

The position of the central pad in relation to the trochleas of tarsometatarsus and metatarsus I in parrots differs from that in Cuculus canorus and woodpeckers (Fig. 1-2). The posterior margins of the central pad in the parrots lie ventral to the joints in the central foot, whereas the posterior margins in the Cuculus canorus and the woodpeckers lie ventral of phalanx I:2 and phalanx IV:5. This depends on differences in the attachment of the central pad to the skeletal elements.

The discussion has stated that the pads in the parrots differ from those in the Cuculus canorus and the woodpeckers in two respects; (i) the relation to the phalanges, and (ii) the attachment to the skeletal elements. The pads are designated in the same way in relation to phalanges and joints, but this does not mean that the pads in the three taxa are homologous. On the contrary, the parrots deviate in fundamental respects, and it must be supposed that the feet in the parrots have a separate evolution from an ancestral bird, which had a primitive, reptilian arrangement of the digits.

The internal anatomy of the foot in birds with zygodactyle feet was thoroughly studied by Steinbacher (1935). He described the insertion of flexor, extensor, abductor, and adductor muscles; the tendon holder of the trochlea for the fourth digit; the capsular ligaments in the third and fourth digit; and the number of articular surfaces in the basal phalanges of the fourth digit. The differences between Cuculidae, Galbulae, Picae, and Psittacidae (classification of Storer 1971) could not be understood from a functional standpoint; instead, they indicated a separate evolution of the zygodactyle feet in the four taxa. My study has shown that the pads in the Psittacidae, obviously have a separate evolution from an ancestral bird type, whereas the evidence in the species of the Cuculidae and Picae is not conclusive.

LITERATURE

- Blume, D. 1963. Die Buntspechte. Vol. 315 in: Die Neue Brehm Bücherei. Ziemsen, Wittenberg Lutherstadt.
- Bock, W.J. & Miller, W.DeW. 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. - Amer. Mus. Nov. 1931:1-45.
- Burt, W.H. 1930. Adaptive modifications in the woodpeckers. - Univ. California Publ. Zool. 32:427-442.
- Dorst, J. 1964. Article 'Parrots'. Pp. 600-602 in Thomson, A.L. (ed.): New Dict. Birds. Nelson, London.
- Goodge, W.R. 1972. Anatomical evidence for phylogenetic relationships among woodpeckers. - Auk 89:65-85.
- Richardson, F. 1942. Adaptive modifications for tree-trunk foraging in birds. - Univ. California Publ. Zool. 46:317-368.
- Scharnke, H. 1930. Physiologisch-anatomisches Studien am Fuss der Spechte. - J. Orn. 78:308-327.
- Steinbacher, G. 1935. Funktionell-anatomische Untersuchungen an Vogelfüssen mit Wendezehe und Rückzehe. - J. Orn. 83:214-282.
- Steinbacher, J. 1964. Article 'Woodpecker'. Pp. 895-897 in Thomson, A.L. (ed.): New Dict. Birds. Nelson, London.
- Stolpe, M. 1932. Physiologisch-anatomische Untersuchungen über die hintere Extremität der Vögel. - J. Orn. 80:161-247.
- Storer, R.W. 1971. Classification of birds. Pp. 1-18 in Farner, D.S. & King, J.R. (eds.): Avian biology. Vol. 1. Academ. Press, New York & London.
- Vaurie, C. 1965. The Birds of the Palearctic Fauna. Non-Passeriformes. Witherby, London.

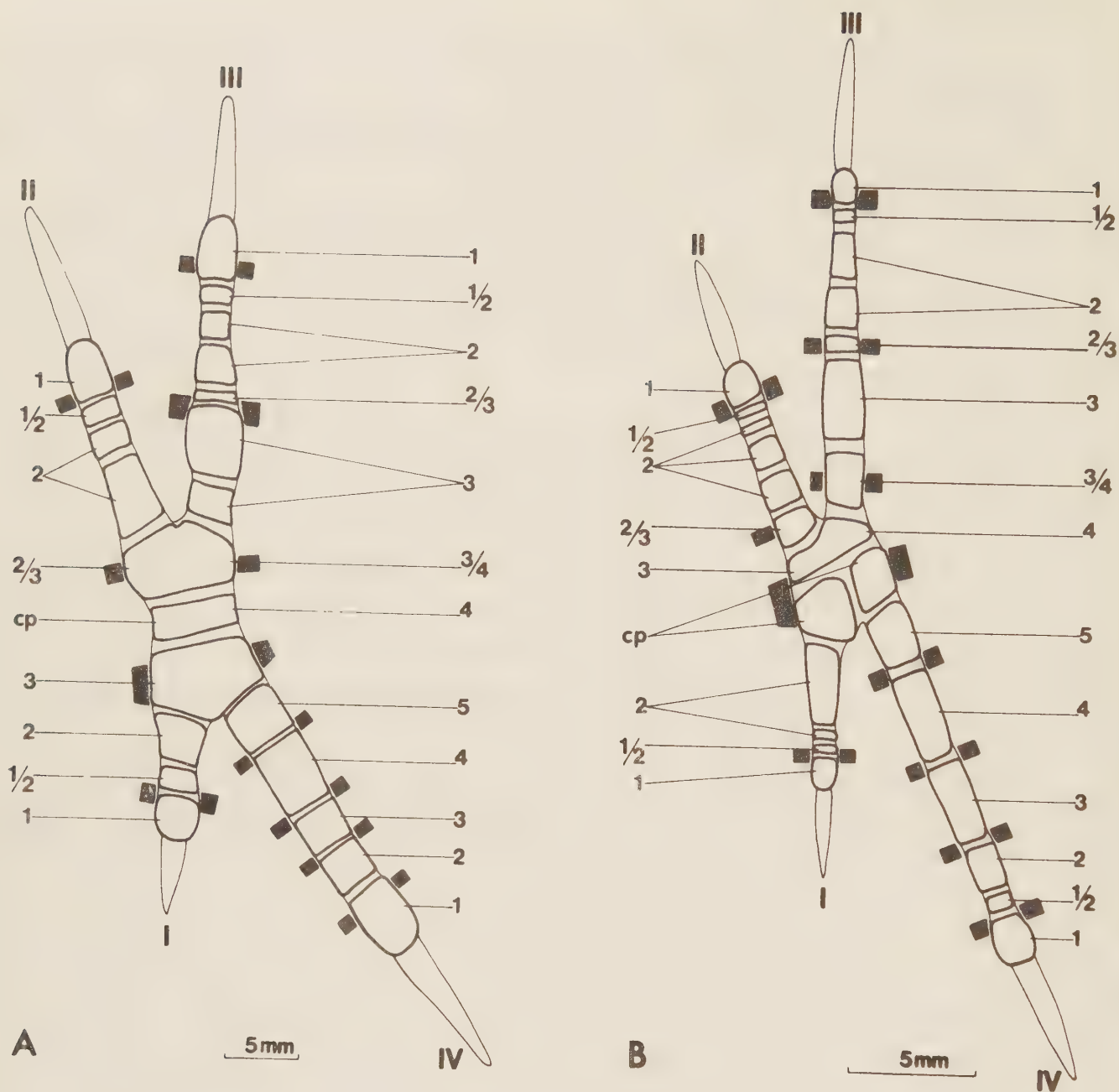


Fig. 1. Pads and folds in (A) *Picus viridis* and (B) *Jynx torquilla*. cp, central pad. Black areas at the sides of the digits indicate the position of joints.

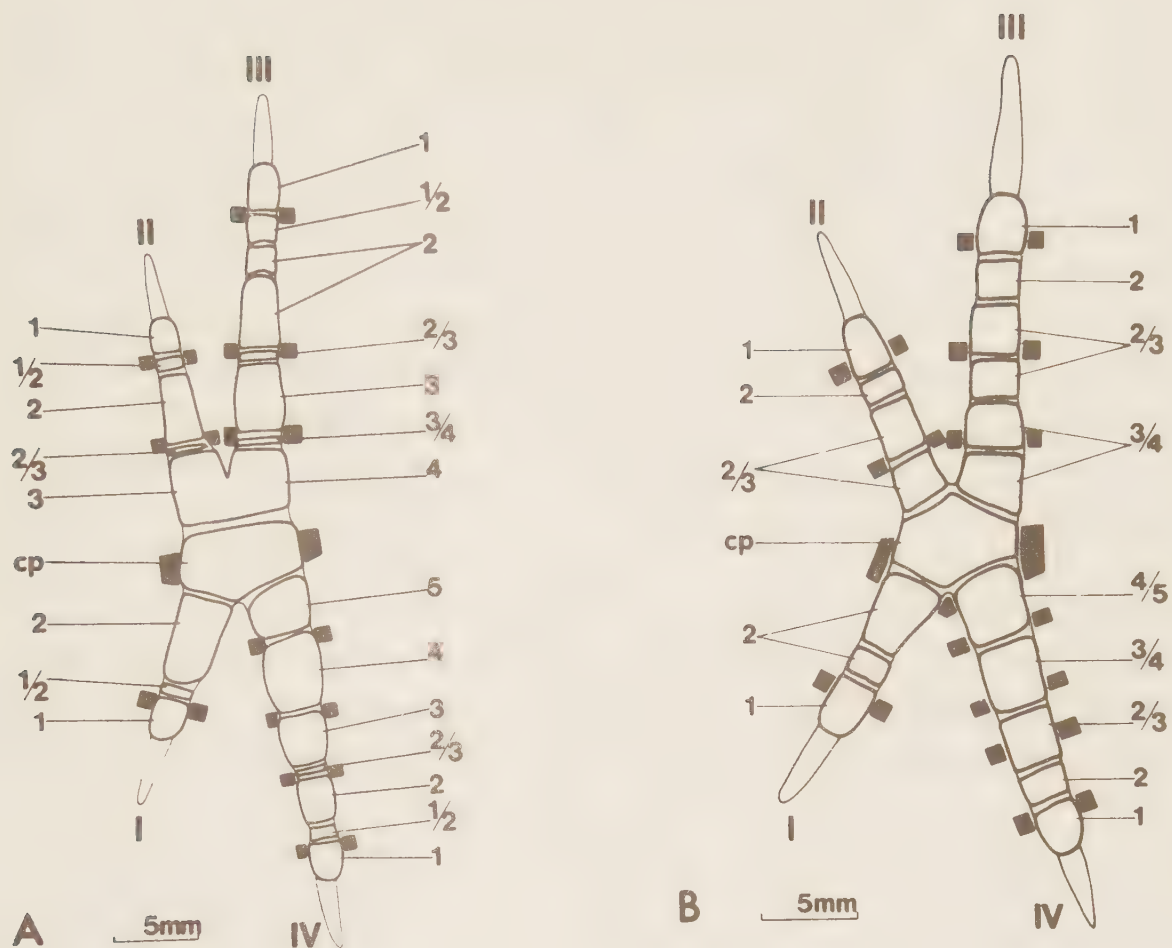


Fig. 2. Pads and folds in (A) *Cuculus canorus* and (B) *Aratinga aurea*. *cp*, central pad. Black areas at the sides of the digit indicate the position of joints.

VI. A functional study of papillae and pads in the foot of passerines, parrots and owls.

ABSTRACT

The papillae in the pads of passerines are connected to one another by means of the stratum corneum, only the top being free to penetrate roughnesses in the bark of branches or twigs. Bundles of collagenous fibres extend from the pads and folds to the phalanges, tendon sheaths, joint capsules, and tendons near their insertions. These fibre bundles attach the plantar skin directly to the skeletal elements. The passerines have large scales which lie as saddles on the digits. Certain of these scales are very firmly attached to the phalanges, and they form an indirect attachment of the pads to the phalanges. The structure of papillae and pads and their firm attachment to the skeletal elements are adapted to resist the great forces exerted on the digits when the bird jumps or flies between branches or twigs.

The papillae in the parrots are free from one another, and many of them are supplied with one or rarely two Herbst sensory corpuscles. The pads are attached by fibre bundles directly to the skeletal elements. The structure of the papillae and the attachment of the pads correlate with the sluggish way of using the foot to grasp twigs or to manipulate food.

The papillae in the owls are free from one another. Certain pads have thick dermis with densely packed collagenous fibres which form a base for the papillae. The large pads are firmly attached by fibre bundles directly to the skeletal elements. The pad in the central part of the foot has a peculiar ligament which attaches it to several skeletal elements. The morphology of papillae and pads and the attachment of pads correlate with the habits of sitting on branches and of grasping prey.

CONTENTS

Introduction

Material and methods

Terminology

Descriptions

 Passerine species

 Parrots

 Owls

Discussion

Abbreviations

Literature

INTRODUCTION

The aim of the present study was to compare the structure of the papillae and the attachment of the pads to the skeletal elements, in species of the three orders Passeriformes, Psittaciformes, and Strigiformes. The functional observations on papillae and pads were made when dissecting the fresh feet. The function was compared with the morphology as seen in histological preparations.

The pads and folds of passerines and parrots are described in earlier studies (pp. 21, 54).

The present study shows that the large scales on the digits have a function in the attachment of the skin to the skeletal elements. This function of the scales has not earlier been described in the literature. Morlion (1968) and Clarke (1972) studied the large scales on the dorsal sides of the digits in passerine species and discussed their taxonomic value. Much greater attention has been paid to the scutellation of the tarsus (Cabanis 1847, Sundevall 1872-73, Reichenow 1871, 1913-14, Gadow & Selenka 1891, Ridgway 1901-1911, Boetticher 1930, Blaszyk 1935, Tyne & Berger 1959). It has been used to diagnose certain groups of passerines, but the taxonomic value seems to be unreliable (Pycraft 1906, Ridgway 1907 p. 336, Blaszyk 1935, Vaurie 1953, Rand 1959, Ames et al. 1968). No functional study of the tarsal scutellation in relation to the muscles and tendons has been carried out, but comments are made by Blaszyk.

MATERIAL AND METHODS

The feet of the following species (number of birds in brackets) were dissected in fresh condition under a stereo microscope: the crow Corvus corone (3), the parrot Poicephalus robustus (1), the parakeet Aratinga aurea (1), and the owl Asio otus (2). The attachment of the skin to the skeletal elements was studied by manipulating the tissues with pins and tweezers. The drawings in Fig. 4, 7, and 10 were made with a camera lucida apparatus in the microscope.

Frozen digits of the mentioned species were cut out into 2-3 mm thick discs. Each disc was placed on a glass slide and studied after thawing. Pressures and tensions, in various directions, were applied on pads, folds, and papillae to see how the papillae behaved and how the skin was attached to the skeletal elements.

The feet decayed for some days in room temperature, and the stratum corneum

was separated from the remaining tissues. The stratum corneum was then manipulated by tweezers; pressures and tensions were applied to see how the stratum corneum behaved.

Feet of the parakeet Aratinga aurea, the owl Asio otus, and the passerines Corvus corone, Erithacus rubecula, Ficedula hypoleuca, Phylloscopus trochilus, and Lanius collurio were fixed in a mixture of 80 per cent alcohol, concentrated formol, and concentrated acetic acid (18:1:1). They were decalcified in 5 per cent nitric acid, embedded in celloidin, serial sectioned in transversel and sagittal planes at 40-60 μ m on a sleigh microtome, and stained with Ehrlich's haematoxylin. Slides of pads from the owl Nyctia scandiaca were kindly supplied by K.G. Wingstrand.

TERMINOLOGY

The pads and folds are designated according to the adjacent phalanx or joint (p. 9).

The general morphology of a papilla is described on p.101 and the embryonic development on p. 6 . The dermal tissue project into the papilla by the primary dermal papilla, which at the top divides into several secondary dermal papillae. The epidermis has two layers, stratum germinativum and stratum corneum. The basal cells of stratum germinativum lie at the dermo-epidermal junction.

Four types of epidermis are distinguished in the present study: scale epidermis, hinge epidermis, papilla epidermis, and body epidermis. Spearman (1966), Cane & Spearman (1967), and Baden & Maderson (1970) studied the histochemistry and X-ray diffraction of the scale and hinge epidermis on the tarsus; Sawyer (1972) described the morphogenesis of the large scales on the anterior tarsus, distinguishing outer and inner scale surfaces. The stratum corneum of the outer scale surface has a glassy appearance in histological preparations, and the fibrous protein gives the β or feather type of X-ray diffraction; this type of epidermis is designated scale epidermis. The flexible inner scale surface, as seen in histological preparations, has a lamellar structure in the stratum corneum and the fibrous protein gives the α or hair type of X-ray diffraction; this epidermis is designated hinge epidermis. The stratum corneum in the papillae has eosine affinity, as has the hinge epidermis, but no lamellar appearance in histological preparations. Certain histochemical reactions in the papillae differ from those in the scale and hinge epidermis (Cane & Spearman 1967). Therefore, I assume that the papillae represent a third type of epidermis, which I designate plantar epidermis. The epidermis of the body and feathered parts of the legs is thin, having only a few layers of horny cells. This type

of epidermis is designated body epidermis. Matoltzy (1969) described the ultrastructure of body epidermis in newly hatched chicks and pointed out that the horny cells differ both structurally and chemically from corresponding epidermis in mammals.

Gadow & Selenka (1891 p. 88), Schaffer (1903), Lubosch (1910), and Cracraft (1971) described the anatomy of phalanges and joints. The phalanx has three parts: head, shaft, and basis. The head has a longitudinal sulcus which divides the head into two condyles. Most of the condyle surface is covered by the joint capsule. The basis has a superior and an inferior tubercle separated by an articular fossa. The distal phalanx has a ventral tubercle at the base of the claw, being the area of insertion for the tendon of the long flexor muscle and functionally acting as a lever arm (Goslov 1972). The articular surface of the proximal phalanges can deviate from the scheme according to the rotatory movements of the digits and the attachment of certain ligaments and muscles.

The phalanges, joint capsules, and tendon sheaths are referred to as the skeletal elements.

Hudson (1937), Holmes (1963), and George & Berger (1966) reviewed the extensive literature on leg muscles and areas of insertion for tendons. The George & Berger terminology is used in the present study.

The direction of the digits refers to a foot resting on a horizontal substrate. Anterior and posterior are in accordance with the direction of the body. The digit has medial, lateral, dorsal, and ventral (plantar) sides.

DESCRIPTIONS

Passerines

Plate IA shows the large scales on tarsometatarsus and metatarsus I in Corvus corone. The dorsal side of the digits is covered with large scales lying like saddles on the digits. The medial and lateral sides of the digit are furnished with small scales of variable form. There is a gradual transition in morphology between the large and the small scales and between the small scales and the papillae in the pad (Madsen & Wingstrand 1959).

Most passerine species are smaller than Corvus corone and have fewer small scales between the large scales and the papillae.

Fig. 1A shows the pads and folds in Corvus corone (p. 27). There are twelve pads related to phalanges (I:1, I:2, II:1, II:2, II:3, III:1, III:2, III:3, IV:1, IV:2, IV:3, IV:4) and one pad in central part of the foot. There are also a number of folds between the pads. Fold I:1/2, II:1/2, III:1/2, and IV:1/2 are

designated as though related to their respective joints; they can also be interpreted as separated parts of pads (p. 33). If the latter interpretation is correct, the fold at the joints have been reduced. Fold IV:4/5 has fused with pad IV:4 and with one of the folds at phalanx III:4.

Fig. 2A shows a diagram of a section through the third digit and pad III:2, and a diagram of a papilla in Lanius collurio. The horny cells in the margin of the papilla are oriented perpendicularly to the surface, and the horny cells in the middle, parallelly. This means that the marginal horny cells form a cylinder in the papilla. These horny cells are connected to the horny cells of the adjacent papilla. In this way, the stratum germinativum of the papillae in a pad form a horny plate. Plate IB shows the deep surface of the stratum germinativum in Corvus corone. The horny plate is flexible but only slightly stretchable; it has cavities occupied by the dermal papillae. As the dermal layer in the pad is thin, it is the horny plate that forms the structural element in the pad. Only the top of the papillae are free and project from the plate. Fig. 2A shows that the stratum germinativum of the pad hinges to the scales in the medial and lateral sides of the digit.

Many pads are supported by subcutaneous connective tissue, which forms a bolster under the skin. The subcutaneous tissue in pad III:2 of Lanius collurio is shown in Fig. 2A. The Corvus corone has extensive fat deposit in vacuoles in the fat cells, but many small passerine species have no fat vacuoles.

Fig. 3A shows a section through fold III:2/3. The papillae are arranged in one row across the digit. Other folds have two, or rarely three, rows of papillae. The papillae in the fold are lower and the secondary dermal papillae shorter than in the papillae of the pad. The surface of the papillae in the fold is often rounded, and the papillae are probably less worn against the substrate than those in the pad.

Fig. 3B shows a section through the furrow between pad III:2 and fold III:2/3. The stratum corneum is as thick as in the pad. There are no secondary dermal papillae. The epidermis in the furrow seems to resemble that in the papillae, which is the plantar type.

The pads and folds are attached directly and indirectly to the skeletal elements: phalanges, joint capsules, tendon sheaths, and tendons near their surfaces of insertion.

The direct attachment of a pad or a fold to the skeletal elements is mediated by collagenous fibre bundles. Fig. 2A, 3A, and 3B show these fibre bundles in pad III:2, fold III:2/3, and the furrow between pad III:2 and fold III:2/3. They extend from the sides of pad III:2 to the ventromedial and ventrolateral surfaces

of the tendon sheath. The capsule at joint III:2/3 has intimate contact with the dermis. The tendon of M. flexor perforans et perforatus digiti III inserts by one branch on ventromedial and one branch on ventrolateral surface of the basis of phalanx III:2; at the insertion, the tendons are intimately connected to the dermis. This means a secondary insertion of the tendon on the skin.

The indirect attachment of pads and folds to the skeletal elements is brought about by the large scales on the dorsal side of the digit. Fig. 2A shows that the scale and the phalanx lie close together. They can hardly be moved in relation to each other, although no distinct fibre bundles extend straight from the scale to the pad. Between the large scales and the small scales and between the small scales and the pad, there is skin with hinge epidermis. Thus the skin forms a cylinder around the digit, and this cylinder is attached to the phalanx by the large scale. This indirect attachment is not shown in Fig. 4, but the contour of the large scales on the dorsal side of the digit is indicated. Pad II:2, III:2, IV:2, IV:3, and IV:4 each have one large scale and pad I:2 has two large scales.

The diagrams in Fig. 4 show the fibre bundles that attach the different pads and folds to the skeletal elements in Corvus corone. The tendon sheaths and ventral part of joint capsules are indicated, but the tendons of the flexor muscles are omitted. The diagrams should be compared with the diagrams of pads and folds in Fig. 1A and the surfaces of insertion of the flexor muscles as indicated in Fig. 1B; the surfaces of insertion for the flexor muscles are described in Table 1 (Hudson 1937, George & Berger 1966).

Pad I:1, II:1, III:1, and IV:1 are attached in the same way. Pad I:1 is intimately attached to the ventral tubercle, anteriorly to the surface of insertion of the long flexor muscle, and to the lateral and medial sides of the phalanx at the base of the claw. Fibre bundles extend from the sides of the pad to the medial and lateral surfaces of phalanx I:1; other fibre bundles extend to the medial and lateral surface of the joint capsule or the medial and lateral surface of the head of phalanx I:2. The last-mentioned bundles were not observed in all the four pads.

Pad II:2, III:2, IV:2, IV:3, and IV:4 are attached in the same way. Fibre bundles extend from the distal part of pad II:2 to the medial and lateral surfaces of the head of phalanx II:2, and from the proximal part of the pad to ventromedial and ventrolateral surfaces of the basis of phalanx II:2. The pad is also attached to the ventromedial and ventrolateral surfaces of the tendon sheath.

Pad I:2 has some peculiar features. Two separate fibre bundles extend from the sides of the distal part of the pad to the sides of the head of phalanx I:2; they pass the joint capsule and attach at the dorsomedial and dorsolateral sur-

faces of the basis of phalanx I:1, close to the elastic automatic extensor of joint I:1/2. This automatic extensor is described by Hudson (1937, p. 51) and George & Berger (1966, p. 455). Functionally this causes a stretching of the pad when phalanx I:1 is bent.

The proximal attachment of pad I:2 is also peculiar. The pad is attached to the medial and lateral surfaces of the basis of phalanx I:2 in a way similar to that in pad II:2, but is also attached to phalanx II:3 and phalanx IV:5. A fibre bundle extends from the medioproximal part of pad I:2 to the medial surface of the basis of phalanx II:3, and a similar fibre bundle extends from the lateroproximal part of pad I:2 to the lateral surface of the basis of phalanx IV:5. The latter fibre bundle is not shown in Fig. 4.

Pad II:3 and pad III:4 are not attached to the basis of the adjacent phalanx. The fibre bundles extend from the proximal part of the pads to the central pad, which is attached to the basis of phalanx II:3 and phalanx III:4.

The central pad is attached to the proximal phalanges of the four digits. A fibre bundle extends from the deep surface of the central pad to the medial surface of the basis of phalanx I:2. Other fibre bundles extend more perpendicularly to the proximal phalanges of the anterior digits.

Fold II:1/2 is attached to the ventromedial and ventrolateral surfaces of the joint capsule near the surface for insertion of the long flexor tendon, but it is also attached to the medial and lateral surfaces of the head of phalanx II:2. Fold III:1/2 is attached to the joint capsule in the same way as fold II:1/2, but no distinct fibre bundles go to the head of phalanx II:2. These differences are possibly individual variations.

There is no fold at joint II:2/3, but one occurs at this site in many other passerine species. The skin in the furrow, however, is attached to the joint capsule in a way similar to that of fold III:2/3.

Parrots

The short tarsus in parrots is covered with small, square to hexagonal, scales. The scales on the dorsal, medial, and lateral sides of the digits are similar to those on the tarsus.

Fig. 5A shows the pads in Aratinga aurea. They are designated in relation to the adjacent phalanx or joint. This designation is made in accordance with the observations in the present study on the attachment of the pads to the skeletal elements. There are no folds. The pattern of pads is uniform in the parrot family, Psittacidae (p. 59).

Fig. 6 shows a diagram of a section through the third digit and the distal

pad III:2/3 and a diagram of a papilla in Aratinga aurea. The papillae are free from one another, and the stratum corneum between the papillae is thinner than that at the top of the papilla. There are several secondary dermal papillae.

Many papillae have one or rarely two Herbst sensory corpuscles. These sensory corpuscles also occur in the scales at the dorsal medial and lateral sides of the digit.

Fig. 6A shows the attachment of pad III:2/3 to the skeletal elements. Heavy bundles of collagenous fibres extend from the margin of the pad to the ventromedial and ventrolateral surface of the phalanx or the tendon sheath. Fewer bundles extend from the central part of the pad through the loose subcutaneous connective tissue to the tendon sheath. The small scales on the medial, dorsal, and lateral sides of the digit are loosely attached to the phalanx. This means that bundles of collagenous fibres form the principle attachment of the pad to the skeletal element, i.e. a direct attachment.

The diagrams in Fig. 7 show the direct attachment of all the pads in Poicephalus robustus. The pads are similar to those in Aratinga aurea (Fig. 5). The tendon sheaths and joint capsules are indicated, but the tendons of the muscles that flex, adduct, or abduct the digits are omitted. The diagrams should be compared with pattern of pads, shown in Fig. 5A. The surfaces for insertion of flexor, adductor, and abductor muscles are projected on the diagram of pads in Fig. 5B. Table 2 describes the surface of insertion. The tendons of the extensor muscles insert asymmetrically on the phalanges, and they contribute to adduction and abduction, but these muscles are excluded from Table 2.

Pad I:1, II:1, III:1, and IV:1 are attached in the same way. Heavy bundles of collagenous fibres extend from the anterior side of pad I:1 to the ventral tubercle anteriorly to the insertion of the long flexor muscle. Fibre bundles also extend from the medial and lateral sides of the pad to the ventromedial and ventrolateral sides of the phalanx. The posterior margin of the pad is attached to the ventromedial and ventrolateral surfaces of the basis of phalanx I:1. Pad II:1, III:1, and IV:1 are also attached to the medial and lateral surfaces of the head of the second phalanx.

Pad II:2 is attached to the ventromedial and ventrolateral surfaces of the basis of phalanx II:1 and to the ventromedial and ventrolateral surfaces of the head and the anterior half of the shaft of phalanx II:2.

Pad II:2/3 is divided into distal pad II:2/3 and proximal pad II:2/3. These pads are attached to the ventromedial and ventrolateral surfaces of the basis and the proximal part of the shaft of phalanx II:2 and also to the ventromedial and ventrolateral surfaces of the head and the distal part of the shaft of

phalanx II:3. There are few fibre bundles to the ventral part of the joint capsule or the tendon sheath.

Pad III:2/3 and pad III:3/4 are both subdivided as pad II:2/3. They are attached to the adjacent phalanges in the same way as pad II:2/3.

Pad IV:2/3 lies ventral to joint IV:2/3. It is attached to the proximal part of the shaft of phalanx IV:2, to the basis of phalanx IV:2, to the head of phalanx IV:3, and to the distal part of the shaft of phalanx IV:3.

Pad IV:3/4 and pad IV:4/5 are attached to the adjacent skeletal elements in the same way as pad IV:2/3.

The central pad is large and is attached to several skeletal structures. It is attached to the basis of phalanx I:2, II:3, and III:4, and also to the ventromedial surface of the proximal half of the shaft of phalanx IV:5. Also it is attached to the surface ventral to trochlea III and to the tubercle medially to trochlea II. The tendon of M. extensor brevis digiti IV does not insert on the fourth digit, which is abducted by M. flexor perforatus digiti IV, but extends between trochlea III and trochlea IV, divides into several fibre bundles, and inserts on the lateral part of the central pad.

Owls

The tarsus and digits in the owls are covered with feathers. The skin below the feathers is thin and similar to that of the body.

Fig. 8A shows the plantar surface of Asio otus. The pads ventral to the joints are prominent and elevated; they are designated in the figure. The papillae in the margins of these pads are not separated from the papillae in the adjacent skin by any gap; thus the owls have no furrows comparable to those in passerines (p. 21) or domestic hen (p. 6). The margins of the elevated pads are indicated by the lines in Fig. 8A.

Fig. 8A shows the normal, relaxed position of the digits. Digit II, III, and IV are held anteriorly and digit I posteriorly. The digits may change direction, however, by sideways movements, which are combined with rotation in the intertarsal joint. Digit I and II may be held posteromedially, and digit III and IV anterolaterally; but digit I and IV may also be held posterolaterally and digit II and III anteromedially (cf. Norberg 1970). The skin between the basal phalanges of digit II, III, and IV is stretchable to allow these sideways movements of the digits.

Some further points in the structure of the digits can be noted. Phalanx 2 in digit II, III, and IV are long and the phalanges proximal to phalanx 2 are short. This correlates with the grasp of prey (Goslow 1972). Phalanx IV:4 and phalanx IV:5

are short and joint IV:4/5 is immovable. Fig. 10 shows how the proximal phalanges in digit IV are held in a downward position.

Fig. 9 shows a diagram of a section through the third digit and pad III:2/3 and a diagram of two papillae in Asio otus. The papillae are free from one another. The stratum corneum is somewhat thicker at the top of the papilla than between the papillae. The stratum germinativum is thin compared with the stratum corneum, and there are only few, short, secondary, dermal papillae at the top of the papillae. Similar structure of the papilla occurs in Nyctia scandiaca, although the stratum corneum in this arctic species is much thicker than in Asio otus.

The dermis in pad II:2/3, III:2/3, III:3/4, IV:2/3, and IV:3/4 is thick and has densely packed collagenous fibres. The dermis has a firm structure and functions as a base for the papillae. The stratum corneum, separated from the dermis, is stretchable.

The pads designated in Fig. 8A are supported by subcutaneous connective tissue with fat deposit. Fig. 9A shows how this tissue is penetrated by a great many collagenous fibre bundles, which attach the pad directly to the skeletal elements. The skin of the medial, dorsal, and lateral sides of the digit is thin and very loosely attached to the phalanges.

The diagrams in Fig. 10 show the direct attachment of the pads to the skeletal elements in Asio otus. The tendon sheaths and joint capsules are indicated, but the tendons of the muscles that flex and rotate the digit are omitted. The diagrams in Fig. 10 should be compared with the diagrams of pads in Fig. 8A and the surfaces of insertion for the muscles that flex, adduct, and abduct the digit as indicated in Fig. 8B; the surfaces of insertion for the muscles are described in Table 3 (Hudson 1937). The tendons of the extensor muscles insert asymmetrically on the phalanges and contribute to the adduction and abduction, particularly to that of the first digit.

Pad I:1, II:1, III:1, and IV:1 are attached in the same way. Pad I:1 is intimately connected to the ventral tubercle of phalanx I:1, anteriorly to the insertion of *M. flexor digitorum longus* and to the medial and lateral sides of phalanx I:1. Pad I:1 is also attached to the medial and lateral surfaces of the joint capsule.

Pad II:2/3 is attached to the medial, ventral, and lateral surfaces of the basis of phalanx II:2 by a large number of fibre bundles; it is also firmly attached to the tendon of *M. flexor perforans et perforatus digiti II* near the surface of insertion, which is a secondary insertion of the tendon on the pad; finally, the pad is attached to the medial and lateral sides of the head of phalanx II:3.

Pad III:2/3 and pad IV:2/3 are attached to the adjacent skeletal elements in the same way as pad II:2/3, but there seems to be fewer fibre bundles. Pad IV:3/4 is more loosely attached to the skeletal elements.

The plantar skin between pad II:1 and pad II:2/3 is loosely attached to the tendon sheath.

Figs. 8A and 10 show the position of the central pad in relation to the phalanges and tarsometatarsus. The anterior margin of the pad lies ventral to trochlea II and the proximal parts of phalanx III:4 and phalanx IV:5. The posterior margin lies ventral to the shaft of phalanx I:2. The pad has a thick dermal layer and a subcutaneous connective layer with fat lobules. The subcutaneous layer is perforated by a large number of collagenous fibre bundles. The dermal or subcutaneous layer of the central pad is attached to a ligament of collagenous fibres, in structure comparable to the tendon of insertion for the flexor muscles. Fig. 8B shows this ligament, which attaches the central pad to the skeletal elements.

The ligament of the central pad extends into the first digit. It is loosely attached to the dermis of the skin ventral to phalanx I:2; it flattens at the distal part of phalanx I:2 and is then perforated by the tendon of *M. flexor hallucis longus*; the ligament inserts on the ventral surface of the basis of phalanx I:1, which is not inserted by *M. flexor hallucis longus*. A similar tendinous ligament in the first digit occurs in cuckoos (Berger 1952, 1953), and is described as an automatic flexor. The ligament in the owls may perhaps act as an automatic flexor, but the principle function is obviously to keep the central pad in position and attach it to the skeletal elements.

Anteriorly, the ligament of the central pad is attached to the following structures: the ventromedial surface of the basis of phalanx II:3; the ventromedial surface of the basis of phalanx III:4; the ventrolateral surface of the basis of phalanx IV:4; and the lateral and dorsolateral surface of the shaft of phalanx IV:5. Posteriorly, the ligament is also attached to the lateral surface of phalanx I:2.

DISCUSSION

The passerines, parrots, and owls were chosen for the present study as they have different types of papillae and pads and different types of attachment of pads to the skeletal elements.

The papillae in the pads of passerines are connected to one another by the stratum germinativum so that they form a horny plate. The horny plate is flexible,

but only slightly stretchable. The top of the papillae project from the horny plate are free to penetrate into roughnesses in the bark of branches or twigs. The long secondary dermal papillae provide a large area of contact at the dermo-epidermal junction and a large number of basal cells. The basal cells are the site for mitotic activity and renewal of epidermal cells. If the mitotic activity is proportional to the number of basal cells, the long secondary dermal papillae indicate a more intense renewal of epidermal cells in the middle of the papilla than in the margin. The horny cells in the middle of the papillae are oriented parallelly to the surface and the horny cells in the margin, perpendicularly.

The papillae in the parrots are free from one another. The stratum corneum between the papillae is somewhat thinner than at the top of the papilla. When a faint pressure is applied, one or a few papillae in a pad move independently to the other papillae. Many papillae are supplied with a Herbst sensory corpuscle, which is sensitive to pressure and vibrations (Schwartzkopf 1949). The structure of the corpuscle, as seen by light and electron microscopy, is described by Quilliam & Armstrong (1963), Quilliam (1966), Saxod (1967, 1968), Nafstad & Anderson (1970). In many birds, the corpuscles are numerous at the interosseous membrane in the upper leg close to the tibia (Schildmacher 1931, Schwartzkopf 1949), where they are affected by vibrations in the substrate, transferred to the corpuscles principally by the long flexor muscles. Schwartzkopff noticed the numerous corpuscles in the pads of parrots. The papillae in the parrots are thus sensitive to touch. The function of the papillae can be compared to the function of the epidermal ridges in the palmar and plantar surfaces of primates, where the Meissner corpuscles have similar position and record the movements of the skin ridges (Cauna 1954).

The papillae in the owls are free from one another. The dermal layer in the pad is thick and has a dense structure of collagenous fibres. The dermis functions as a base for the papillae. The stratum corneum, separated from the other skin tissues, is easily stretchable. The stratum germinativum in the papillae is thin, and the secondary dermal papillae are short or lacking. This indicates that the renewal of epidermal cells is equally large in the different parts of the papilla. The horny cells in owls have a more homogeneous and less striated appearance than the horny cells in passerines and parrots. The content of the horny cells in owls are possibly different, for instance, in the content of keratin protein, but no histochemical or ultrastructural studies have been carried out to verify this.

The pads in the passerines are very firmly attached to the skeletal elements, both directly by bundles of collagenous fibres and indirectly by the attachment

of the large scales to the phalanges. The pads in the parrots and owls are attached principally or exclusively in the direct way. The attachment of the pads is correlated with the pattern of pads. This is discussed from comparative morphological aspects in two other studies (p. 54, 81).

The structure and function of the papillae and pads are evidently correlated with the habits of the birds. The passerines are preferably tree-living birds that agilely jump or fly between branches or twigs. The feet are exposed to great external forces that cause pressures and tensions in the skin tissue. The connection of the papillae in a pad, forming a horny plate, and the firm direct and indirect attachment of the pad to the skeletal elements are adaptations to resist these external forces. The parrots move in a more sluggish way on the twigs, using the feet and the beak in co-operation to climb. They manipulate the food - consisting of fruits, nuts, and other vegetables - with the feet and carry it to the beak. The structure of the papilla and the occurrence of Herbst sensory corpuscles are clearly correlated with these habits. The owls perch on branches, waiting for prey. The papillae are free and conelike; the pads at the joints are prominent with a dense dermal layer, which functions as a base for the papillae. The pads are firmly attached to the skeletal elements, including the tendons of the flexor muscles. The structure of the papillae and pads is correlated with the habit of grasping branches and prey.

ABBREVIATIONS

The following abbreviations are used in the figures. Muscles:

abdII, M. abductor digiti II; addII, M. adductor digiti II; abdIV, M. abductor digiti IV; ebIV, M. extensor brevis digiti IV; edl, M. extensor digitorum longus; fdl, M. flexor digitorum longus; fhb, M. flexor hallucis brevis; fhl, M. flexor hallucis longus; fpII, M. flexor perforatus digiti II; fpIII, M. flexor perforatus digiti III; fpIV, M. flexor perforatus digiti IV; fppII, M. flexor perforans et perforatus digiti II; fppIII, M. flexor perforans et perforatus digiti III;

Other structures:

bc, basal cell; cp, Central Pad; cpl, central pad ligament; d, dermis; f, feather; Hc, Herbst corpuscle; mt I, metatarsus I; p, subcutaneous tissue of pad; s, subcutaneous tissue; ph, phalanx; sc, stratum corneum; sg, stratum germinativum; tb, tubercle medial to Trochlea II in parrots; th, tendon holder at Trochlea IV in parrots; tmt, tarsometatarsus; tr, trochlea; ts, tendon sheath;

LITERATURE

- Ames, P.L., Heimerdinger, M.A. & Warter, S.L. 1968. The anatomy and systematic position of the antpipits Conopophaga and Corythopis. - Postilla 114:1-32.
- Baden, H.P. & Maderson, P.F.A. 1970. Morphological and biophysical identification of fibrous proteins in the amniotic epidermis. - J. Exp. Zool. 174:225-232.
- Berger, A.J. 1952. The comparative functional morphology of the pelvic appendage in three genera of Cuculidae. - Amer. Midland Nat. 47:513-605.
- Berger, A.J. 1953. On the locomotor anatomy of the Blue Coua, Coua caerulea. - Auk 70:49-83.
- Blaszyk, P. 1935. Untersuchungen über die Stammesgeschichte der Vogelschuppen und Federn und über die Abhängigkeit ihrer Ausbildung am Vogelfuss von der Funktion. - Morph. Jahrb. 75:483-567.
- Boetticher, H. von. 1930. Morphologische und phylogenetische Studien über die hornige Fussbekleidung der Vögel. - Jenaische Z. Naturwiss. 64:377-448.
- Cabanis, J. 1847. Ornithologische Notizen, I+II. - Arch. Naturgesch. (Erichson, Berlin) 13:186-256, 308-352.
- Cane, A.K. & Spearman, R.I.C. 1967. A histochemical study of keratinization in the domestic fowl (Gallus gallus). - J. Zool., London 153:337-352.
- Cauna, N. 1954. Nature and function of the papillary ridges of the digital skin. - Anat. Rec. 119:449-468.
- Clarke, G.A. 1972. Passerine foot-scutes. - Auk 89:549-558.
- Cracraft, J. 1971. The functional morphology of the hind limb of the domestic pigeon, Columba livia. - Bull. Amer. Mus. Nat. Hist. 144:171-268.
- Gadow, H. & Selenka, E. 1891. Vögel. I. Anatomischer Teil. In H.G. Bronn (ed.): Klassen und Ordnungen des Thier-Reichs. Vol. VI:4. C.F. Winter, Leipzig.
- George, J.C. & Berger, A.J. 1966. Avian myology. Academic Press, New York.
- Goslow, G.E. 1971. The attack and strike of some North American raptors. - Auk 88: 815-827.
- Goslow, G.E. 1972. Adaptive mechanisms of the raptor pelvic limb. - Auk 89:47-64.
- Hudson, G.C. 1937. Studies on the muscles of the pelvic appendages in birds. - Amer. Midland Nat. 18:1-108.
- Holmes, E.B. 1963. Variation in the muscles and nerves of the leg in two genera of grouse (Tympanuchus and Pedioecetes). - Univ. Kansas Publ. Mus. Nat. Hist. 12:363-474.
- Lubosch, W. 1910. Bau und Entstehung der Wirbeltiergelenke. G. Fischer, Jena.
- Madsen, H. & Wingstrand, K.G. 1959. Some behavioural reactions and structures enabling birds to endure winter frost in arctic regions. - Vidensk. Meddel. Dansk Naturhist. Foren. 120:15-23.
- Matoltsy, A.G. 1969. Keratinization of the avian epidermis, an ultrastructural study of the newborn chick skin. - J. Ultrastr. Res. 29:438-458.
- Morlion, M.L. 1968. The podotheca of some African genera of Ploceidae. - Biol. Jaarb. (Gent) 36:159-168.
- Nafstad, P.H.J. & Andersen, A.E. 1970. Ultrastructural investigation on the innervation of the Herbst corpuscles. - Zeitschr. Zellforsch. 103:109-114.

- Norberg, R.Å. 1970. Hunting technique of Tengmalms owl, Aegolius funereus (L). - Ornith. Scand. 1:51-64
- Pycraft, W.P. 1906. Contribution to the osteology of birds. Part VIII. The "Tracheophone" Passeres; with remarks on families allied hereto. - Proc. Zool. Soc. London 1:133-159.
- Quilliam, T.A. 1966. Unit design and array patterns in receptor organs. Pp. 86-112 in de Reuck, A.V.S. & Knight, J. (eds.): Touch, heat and pain, a Ciba foundation symposium. J. & A. Churchill, London.
- Quilliam, T.A. & Armstrong, J. 1963. Mechanoreceptors. - Endeavour 22:55-60.
- Rand, A.L. 1959. Tarsal scutellation of song birds as a taxonomic character. - Wilson Bull. 71:274-277.
- Reichenow, A. 1871. Die Fussbekleidung der Vögel. - J. Ornithol. 19:401-458.
- Reichenow, A. 1913-14. Die Vögel. Handbuch der systematischen Ornithologie. Vol. 1+2. F. Enke, Stuttgart.
- Ridgway, R. 1901-1911. The birds of North and Middle America. Parts 1-5. - Bull. U.S. Nat. Mus. 50.
- Sawyer, R.H. 1972. Avian scale development. I. Histogenesis and morphogenesis of the epidermis and dermis during formation of the scale ridge. - J. Exp. Zool. 181:365-384.
- Saxod, R. 1967. Histogenèse des corpuscules sensoriels cutanés chez le poulet et le canard. - Arch. Anat. Microscop. Morphol. Experiment. 56:153-166.
- Saxod, R. 1968. Ultrastructure des corpuscules sensoriels cutanés de Herbst et de Grandry chez le canard. - Arch. Anat. Microscop. Morphol. Expériment. 57:379-400.
- Schaffer, J. 1903. Über die Sperrvorrichtung an den Zehen der Vögel. - Zeitschr. Wiss. Zool. 73:377-428.
- Schildmacher, H. 1931. Untersuchungen über die Funktion der Herbstschen Körperchen. - J. Ornithol. 79:374-415.
- Schwartzkopff, J. 1949. Über Sitz und Leistung von Gehör und Vibrationssinn bei Vögeln. - Zeitschr. vergl. Physiol. 31:527-608.
- Spearman, R.I.C. 1966. The keratinization of epidermal scales, feathers and hairs. - Biol. Rev. 41:59-96.
- Sundevall, C.E. 1872-73. Methodi naturalis avium disponendarum tentamen. Samson & Wallin, Stockholm.
- Van Tyne, J. & Berger, A.J. 1959. Fundamentals of ornithology. J. Wiley & Sons, New York.
- Vaurie, C. 1953. A generic revision of flycatchers of the tribe Muscicapini. - Bull. Amer. Mus. Nat. Hist. 100:453-538.

Table 1. Areas of insertion for the tendons of flexor muscles in Corvus corone.

Muscle and action	Insertion
M. fl. hallucis longus (flexion)	inserts on ventral tubercle of phalanx I:1, and by minor vincula on ventral surface of the basis of phalanx I:1 and on ventromedial and ventrolateral surfaces of head of phalanx I:2.
M. fl. hallucis brevis	the tiny muscle inserts by fleshy fibres on the proximal end of metatarsal cartilage of digit I, which is attached at the basis of phalanx I:2.
M. fl. digitorum longus (flexion)	trifurcates to digit II, III, and IV, and inserts in the same way as the tendon of M. fl. hallucis longus.
M. fl. perforans et perforatus digit II (flexion)	inserts singly on ventromedial surface of the basis of phalanx II:2 and continues as enforcement of ventromedial part of the bone fascia of phalanx II:2.
M. fl. perforatus digiti II (flexion)	inserts by one branch on ventromedial surface and by a second branch on medial half of ventral surface of the basis of phalanx II:3.
M. fl. perforans et perforatus digiti III (flexion)	inserts on ventromedial and ventrolateral surfaces of the basis of phalanx III:2.
M. fl. perforatus digiti III (flexion)	inserts on whole ventral surface of the basis of phalanx III:3.
M. fl. perforatus digiti IV (flexion)	inserts by small branches on ventromedial and ventrolateral surfaces of the basis of phalanx IV:4; inserts by a major branch on the whole ventral surface of the basis of phalanx IV:3 and continues as enforcement of ventromedial and ventrolateral part of bone fascia of phalanx IV:3 for one third of its length; does not insert on phalanx IV:2.

Table 2. Areas of insertion for the tendons of flexion and rotation muscles in Poicephalus robustus.

Muscle and action	Insertion
M. fl. hallucis longus (flexion)	inserts on ventral tubercle of phalanx I:1; no vinculum.
M. fl. hallucis brevis (abduction)	inserts on lateral surface of the basis of phalanx I:2.
M. fl. digitorum longus (flexion)	trifurcates to digit II, III, and IV and inserts in the same way in the three digits: the main tendon inserts on ventral tubercle of phalanx 1 and a tiny vinculum on ventral surface of head of phalanx 2.
M. fl. perforans et perforatus digiti II (flexion and adduction)	inserts on ventral surface of the basis of phalanx II:2 and ventromedial surface of head of phalanx II:3.
M. fl. perforatus digiti II (flexion)	inserts on ventrolateral and ventromedial surface of the basis of phalanx II:3.
M. fl. perforans et perforatus digiti III (flexion)	inserts on whole ventral surface of the basis of phalanx III:2.
M. fl. perforatus digiti III (flexion and adduction)	inserts by a major branch on ventromedial and a minor branch on ventrolateral surface of the basis of phalanx III:3.
M. fl. perforatus digiti IV (flexion and abduction of the posteriorly directed digit)	inserts on ventral surface of the basis of phalanx IV:2; on ventromedial surface of the basis of phalanx IV:3; and on ventromedial surface of the basis of phalanx IV:4 (description as though digit were directed anteriorly).
M. abductor digiti IV (flexion and adduction of the posteriorly directed digit)	inserts partly fleshy on the tuberosity in proximal half of ventrolateral surface of the basis of phalanx IV:5 (description as though the digit were directed anteriorly).

Table 3. Areas of insertion for the tendons of flexion and rotation muscles in Asio otus

Muscle and action	Insertion
M. fl. hallucis longus (flexion)	inserts on ventral tubercle of phalanx I:1; no vinculum to head of phalanx I:2 or joint capsule.
M. fl. hallucis brevis (flexion)	inserts by one branch on lateral crista of ventral basis and a second branch on medial crista of ventral basis of phalanx I:2.
M. fl. digitorum longus (flexion)	trifurcates to digit II, III, and IV, and inserts in the same way as M. fl. hallucis longus.
M. fl. perforans et perforatus digiti II (flexion and probably adduction)	inserts on ventromedial and ventrolateral surface of the basis of phalanx II:2; the medial branch is thicker than the lateral.
M. fl. perforatus digiti II (flexion and probably abduction)	inserts by the principle branch on ventrolateral surface of the basis and by a minor branch on medial half of ventral basis of phalanx II:3.
M. abductor digiti II (adduction)	inserts by fleshy fibres on medial surface of the basis of phalanx II:3.
M. adductor digiti II (flexion and abduction)	inserts on the lateral crista of ventral basis of phalanx II:3.
M. fl. perforans et perforatus digiti III (flexion and probably abduction)	inserts on ventromedial and ventrolateral surface of the basis of phalanx III:2; the tendon on the lateral side is somewhat thicker than that on the medial side.
M. fl. perforatus digiti III (flexion and probably adduction)	inserts on lateral and medial surface of ventral basis of phalanx III:3; the tendon on medial side is somewhat heavier than on lateral side.
M. fl. perforatus digiti IV (flexion)	inserts by one branch on medial and lateral surface of the basis of phalanx IV:3 and by a second branch on the whole ventral surface of phalanx IV:2. There is no insertion on phalanx IV:4 or phalanx IV:5.

Table 3, continued

Muscle and action	Insertion
M. abductor digiti IV (abduction)	inserts on the lateral surface of the basis of phalanx IV:5; the fibres continue as enforcement of bone fascia of phalanx IV:5 and phalanx IV:4.
M. extensor brevis digiti IV (adduction)	passes a bony canal between trochlea III and trochlea IV and inserts on the medial surface of the basis of phalanx IV:5 and continues as enforcement of bone fascia of phalanx IV:5 and phalanx IV:4.

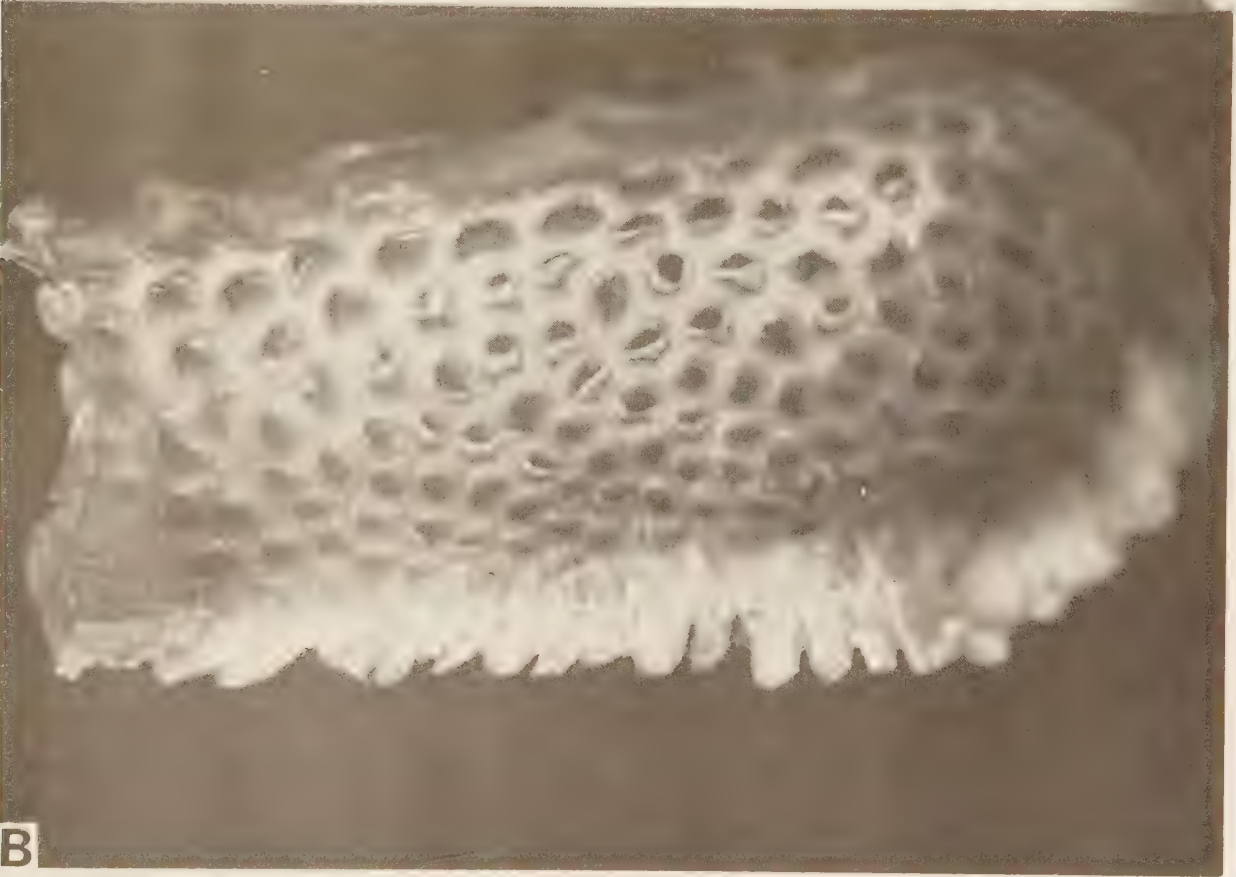
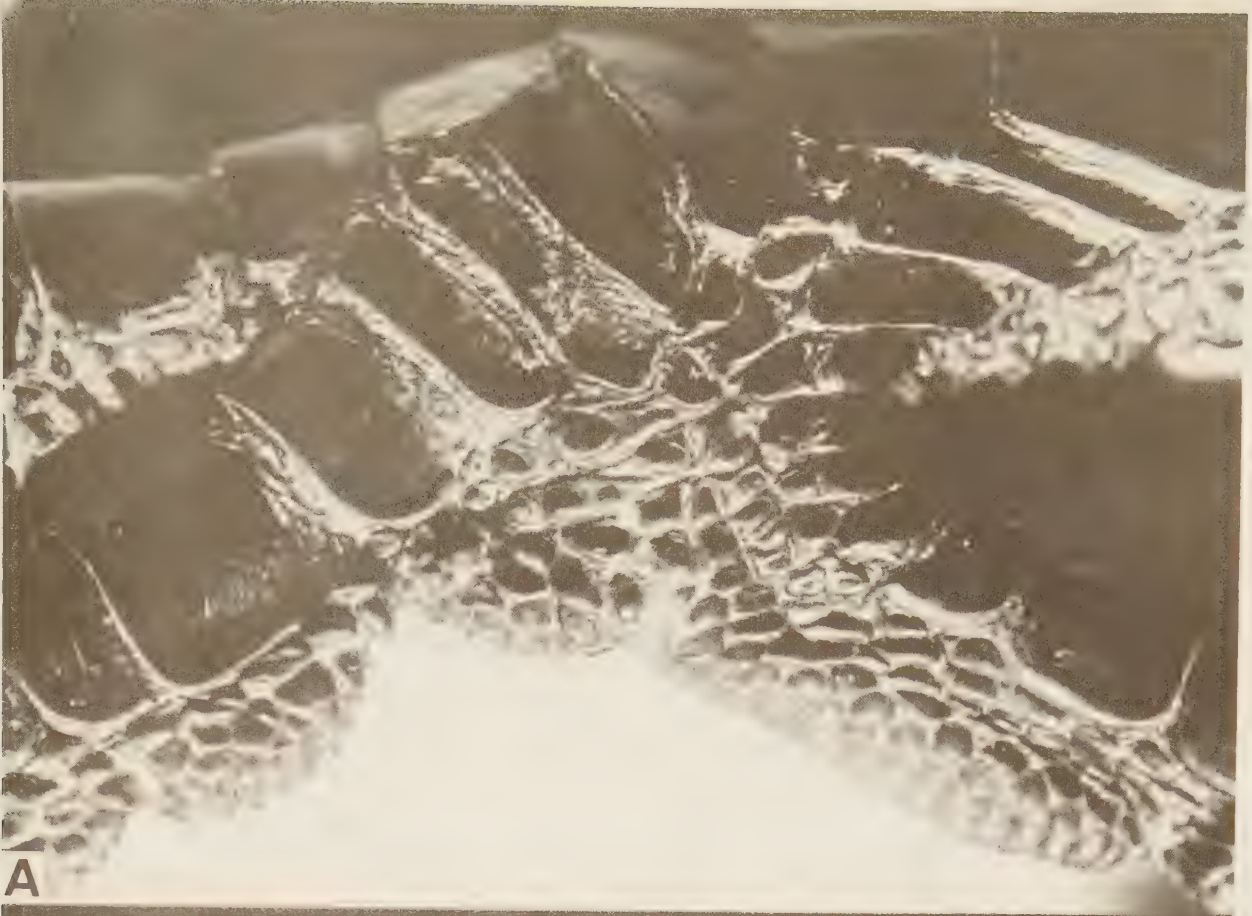


Plate I. (A) Medial view of right foot in Corvus corone, showing the large scales on the dorsal sides of the digits, the small scales on the medial sides, and the papillae and pads on the ventral sides. (B) The stratum corneum of pad I:2 as seen from the deep surface. The papillae are connected to one another, and only the top of the papillae are free. The holes have been occupied by the dermal papillae and the stratum germinativum; remnants of stratum germinativum are seen in certain papillae.

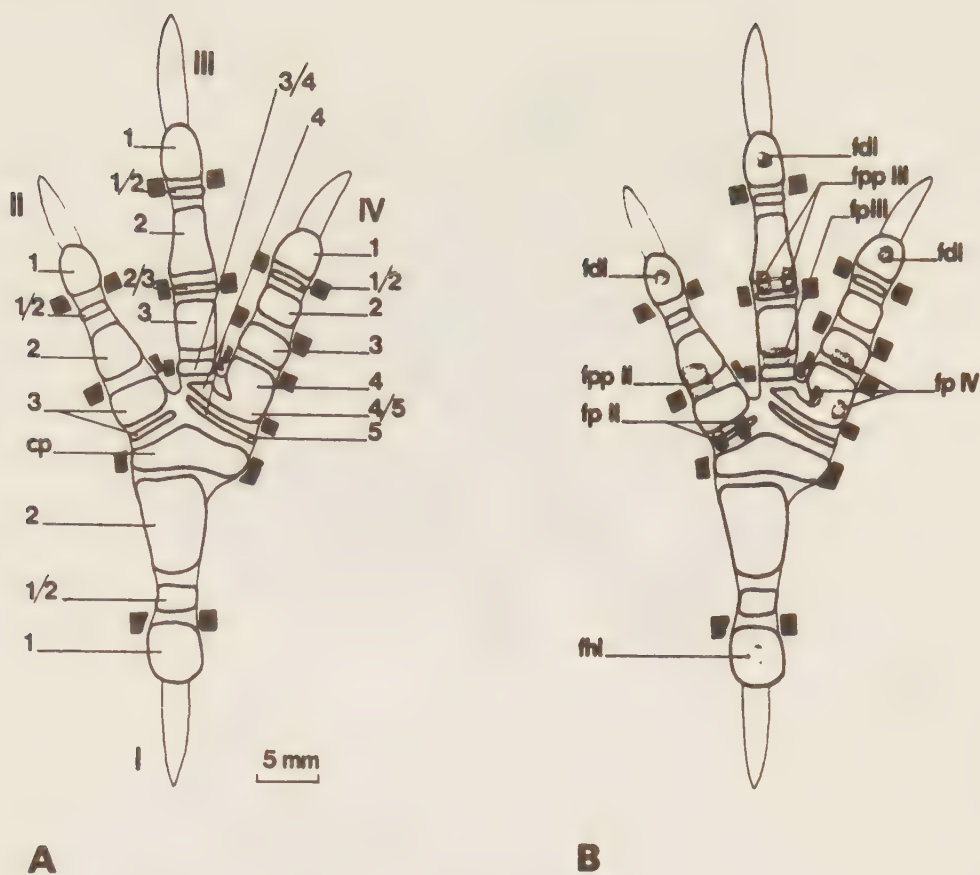


Fig. 1. Diagrams of plantar foot in Corvus corone. (A) designation of pads and folds, (B) areas of insertion for the flexor muscles projected on the pads and folds (dotted areas). Black areas at the sides of the digit indicate the position of joints. For abbreviations, see p. 74.

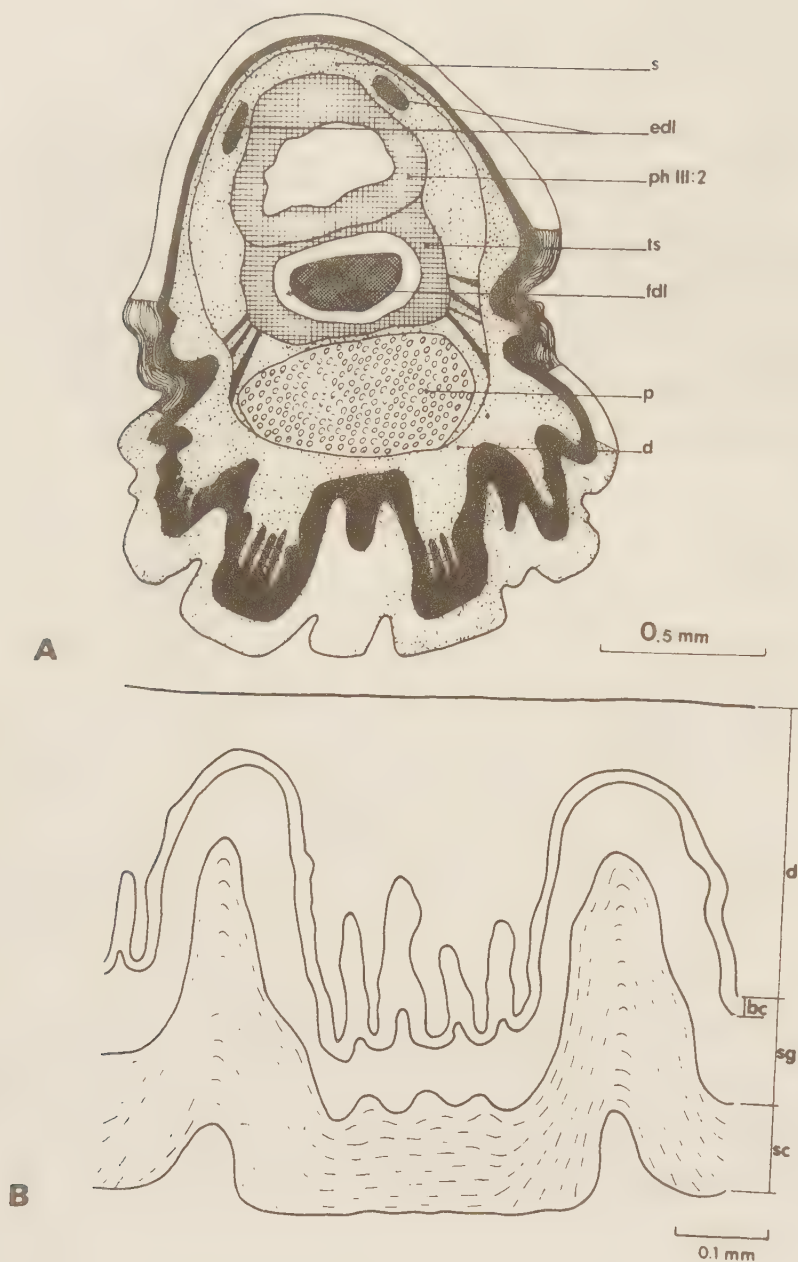


Fig. 2. (A) Diagram of transversel section through pad III:2 in *Lanius collurio*. The bundles of collagenous fibres, attaching the pad directly to the skeletal elements, are indicated by lines. Stratum germinativum is indicated black and stratum corneum according to the type of epidermis: dots for plantar epidermis, lines for hinge epidermis, and blank for scale epidermis. (B) Diagram of a papilla. The orientation of the horny cells is indicated by lines. For abbreviations, see p. 74.

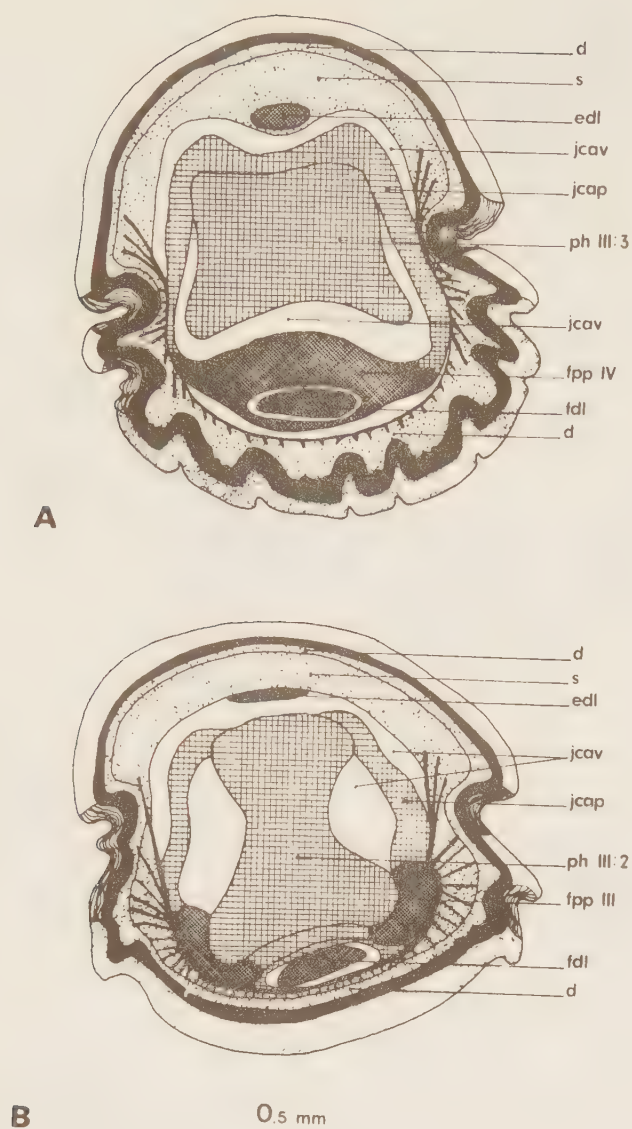


Fig. 3. Diagram of cross sections through the third in digit in Lanius collurio, (A) through fold III:2/3, and (B) through the furrow between pad III:2 and fold III:2/3. The bundles of collagenous fibres that attach the plantar skin directly to the skeletal elements are indicated by lines. Stratum germinativum is indicated black and stratum corneum according to the type of epidermis: dots for plantar epidermis, lines for hinge epidermis, and blank for scale epidermis. For abbreviations, see p. 74.

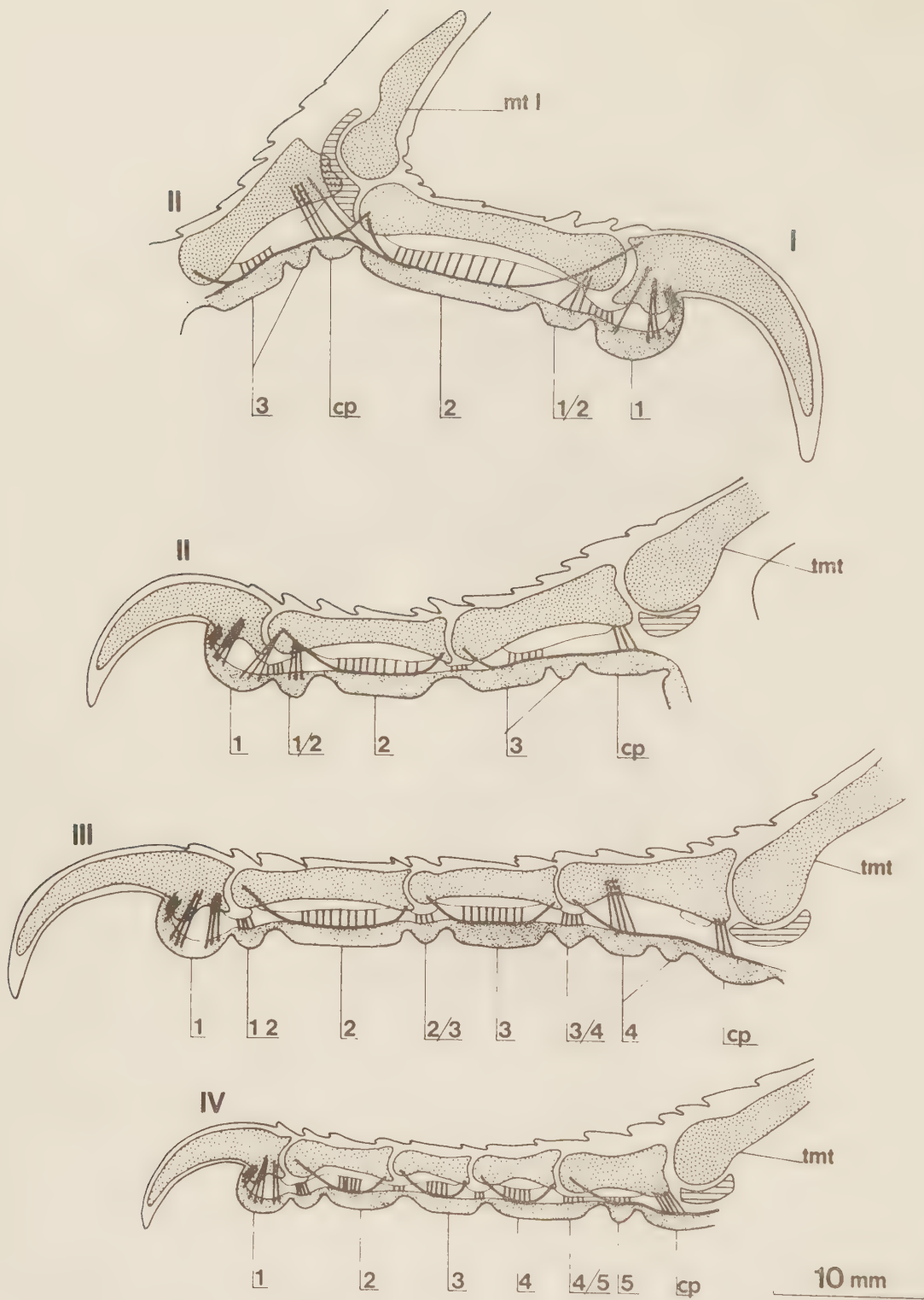


Fig. 4. Diagrams of the right foot in *Corvus corone*, showing the direct attachment of pads and folds (dense spots) by bundles of collagenous fibres (lines) to phalanges (spots) and to joint capsules and tendon sheaths (thin lines). Horizontal lines indicate the fibrous metatarsal cartilage. For abbreviations, see p. 74.

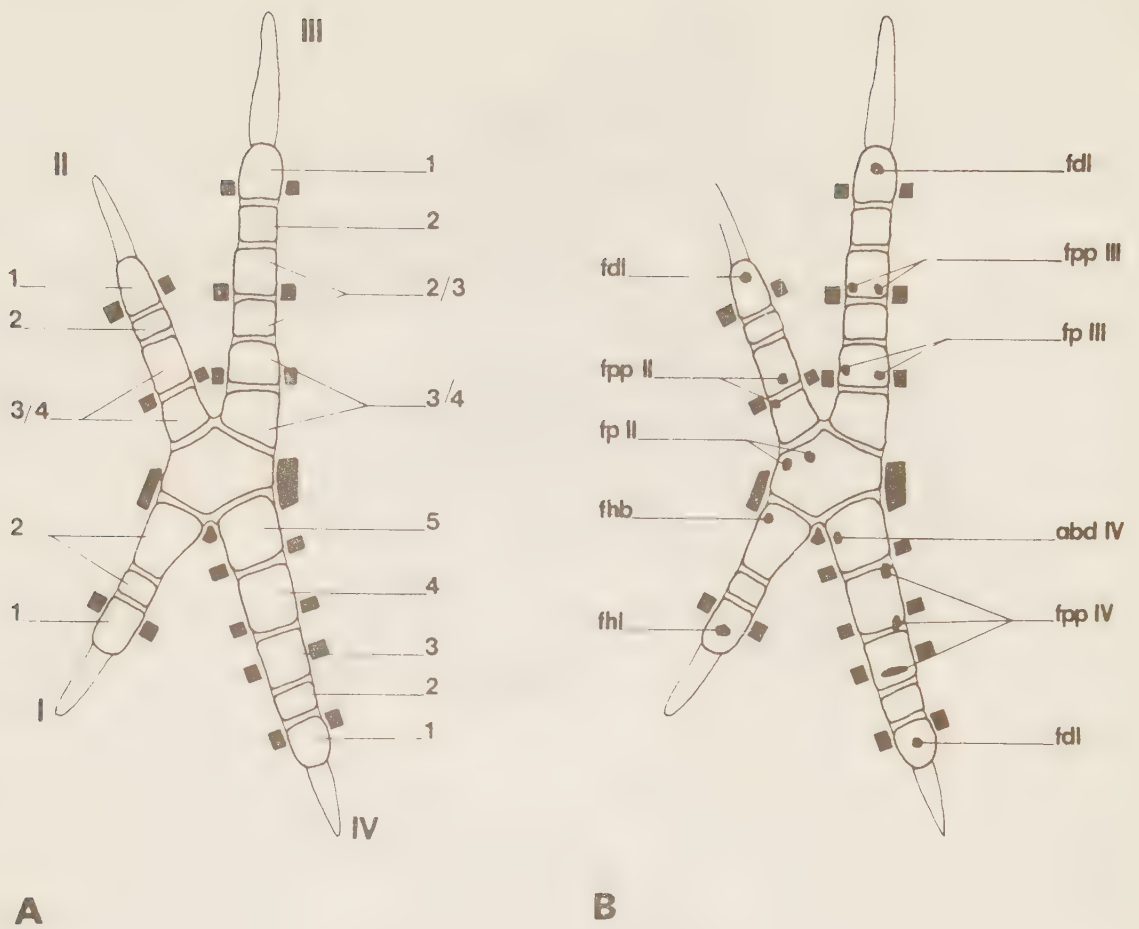


Fig. 5. Diagrams of plantar foot in Aratinga aurea. (A) Designation of pads, (B) surfaces of insertion for the muscles that flex, adduct, and abduct the digits, projected on the pads (dotted areas). Black areas at the sides of the digit indicate the position of joints. For abbreviations, see p. 74.

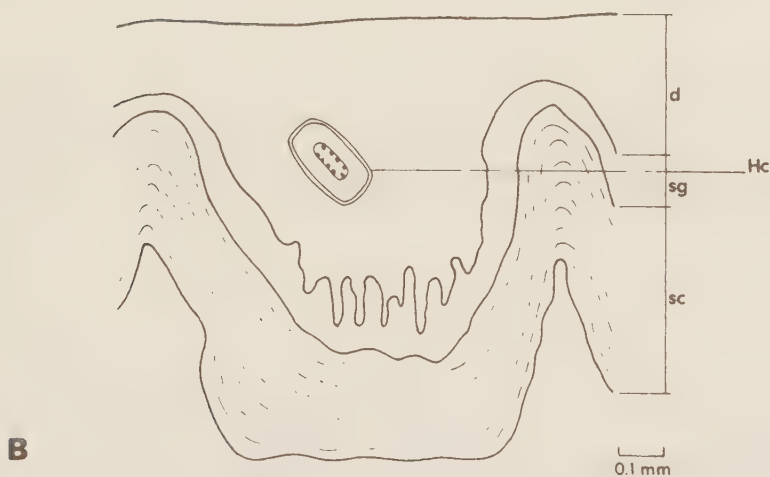
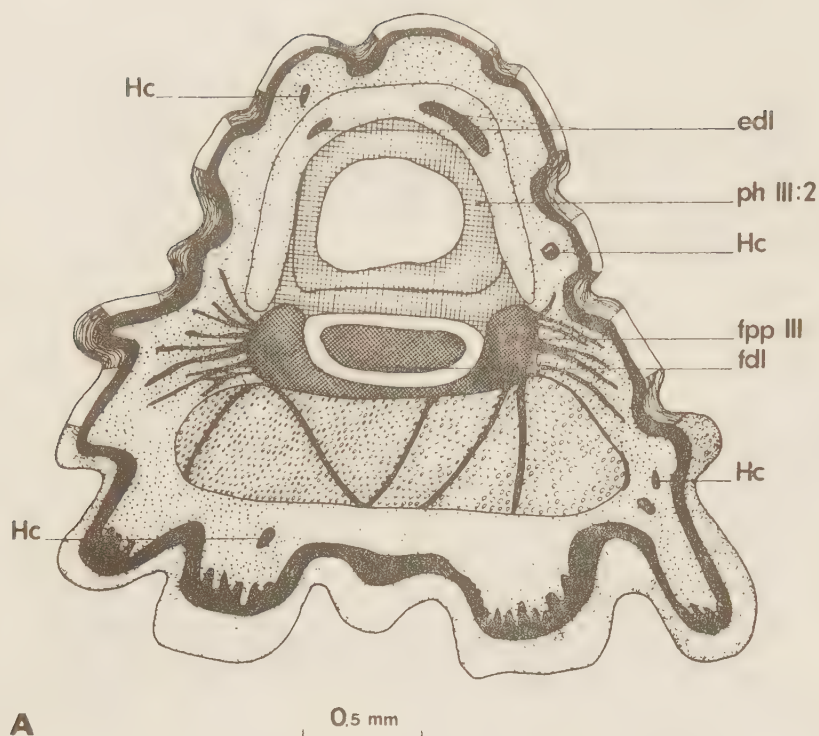


Fig. 6. (A) Diagram of cross section through the third digit and distal pad III:2/3 in *Aratinga aurea*. The bundles of collagenous fibres that attach the skin directly to the skeletal elements are indicated by lines. Stratum germinativum is indicated black and stratum corneum according to the type of epidermis: dots for plantar epidermis, lines for hinge epidermis, and blank for scale epidermis. (B) Diagram of papilla in *Aratinga aurea*. The orientation of the horny cells is indicated by lines in the stratum corneum. For abbreviations, see p. 74.

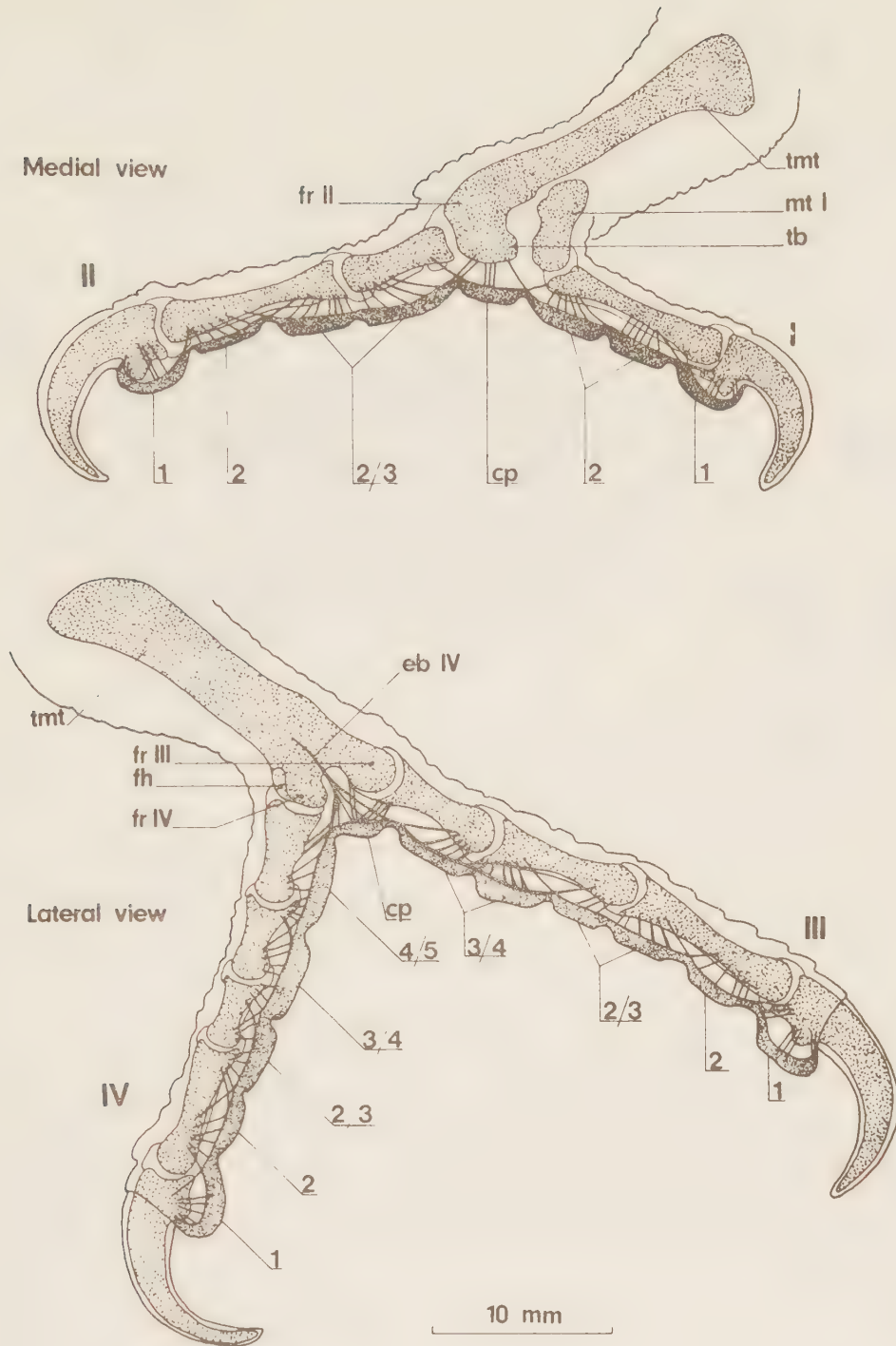


Fig. 7. Diagrams of the right foot of *Poicephalus robustus*, showing the bundles of collagenous fibres (lines) that attach the pads (dense spots) to the phalanges (spots) and to joint capsules or tendon sheaths (thin lines). For abbreviations, see p. 74.

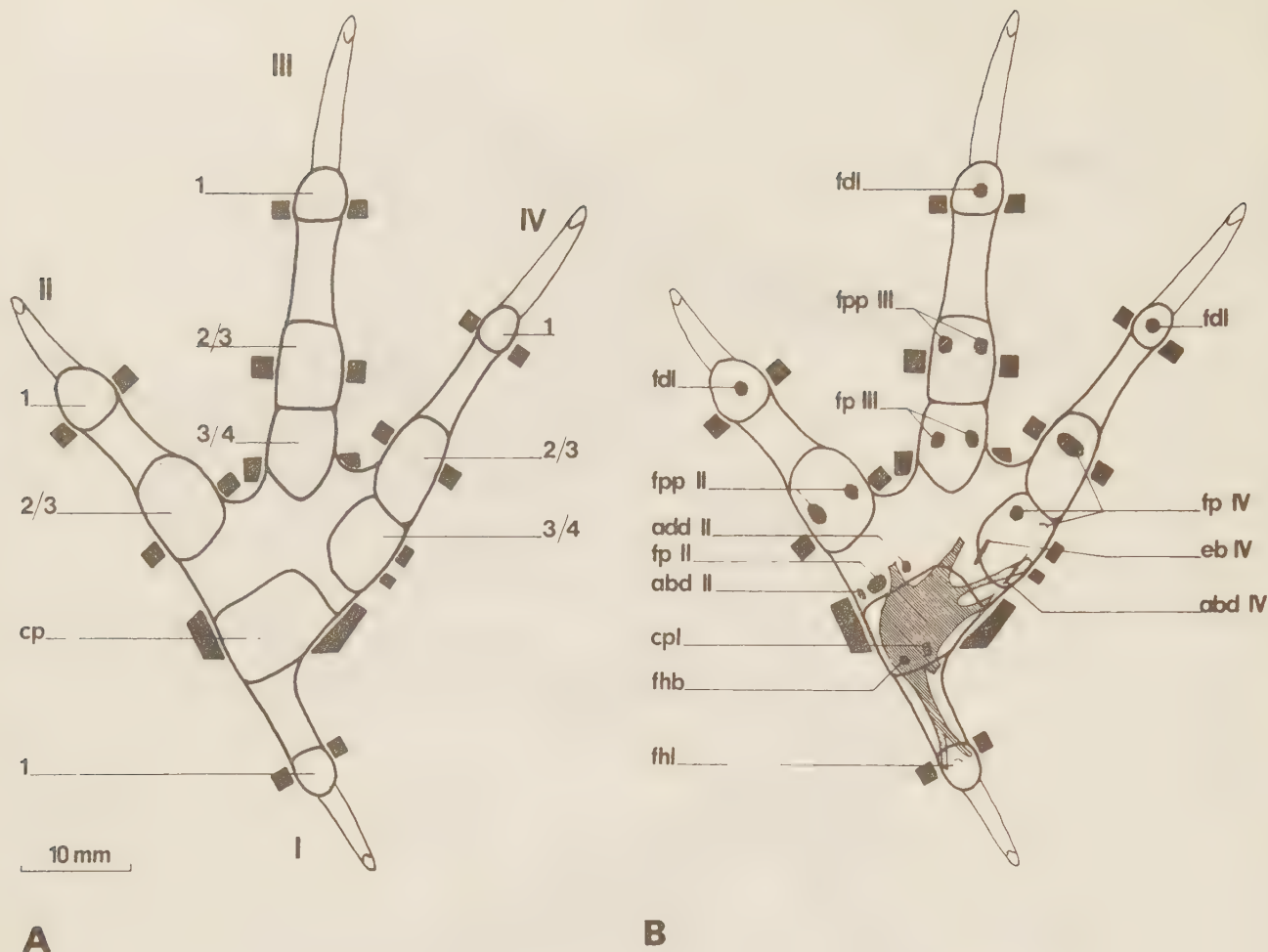


Fig. 8. Diagrams of plantar surface in *Asio otus*. (A) designation of pads, (B) surfaces of insertion for the muscles that flex, adduct, and abduct the digits, projected on the pads (dotted areas); the ligament of the central pad is indicated by lines. For abbreviation, see p. 74.

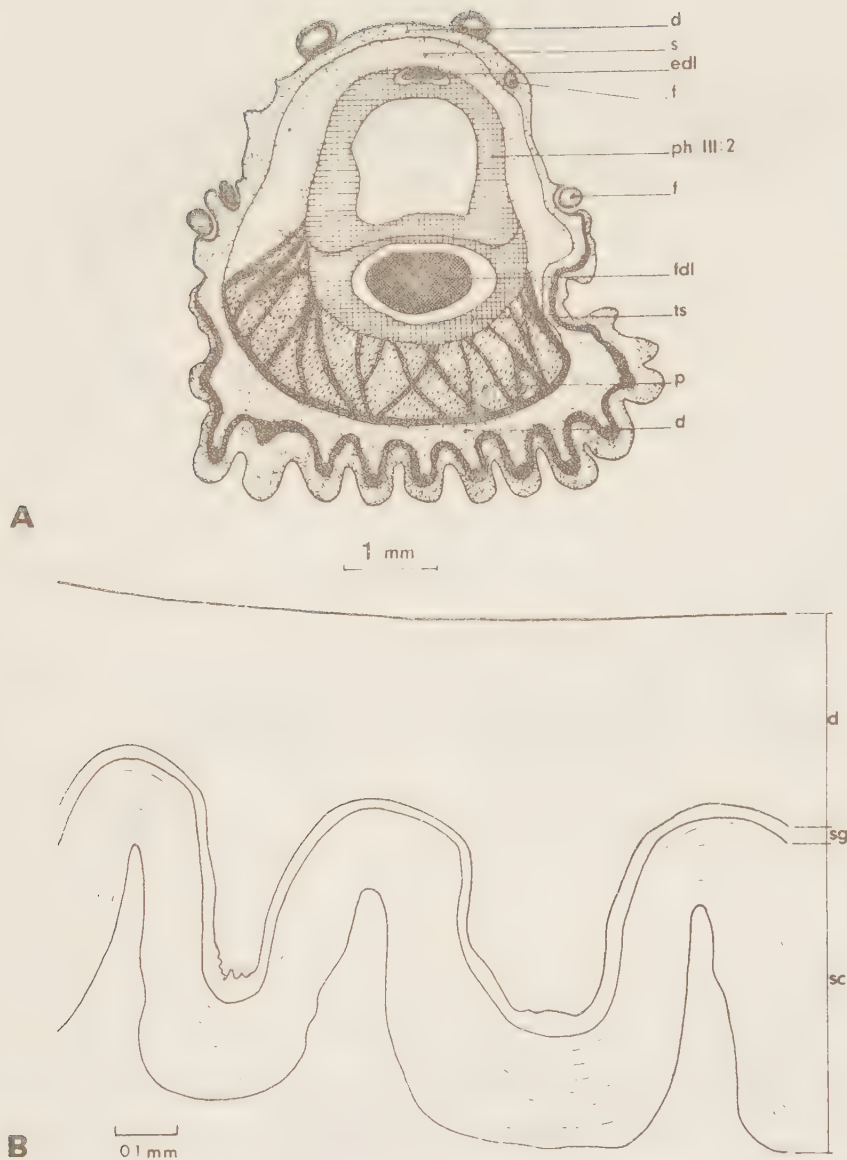
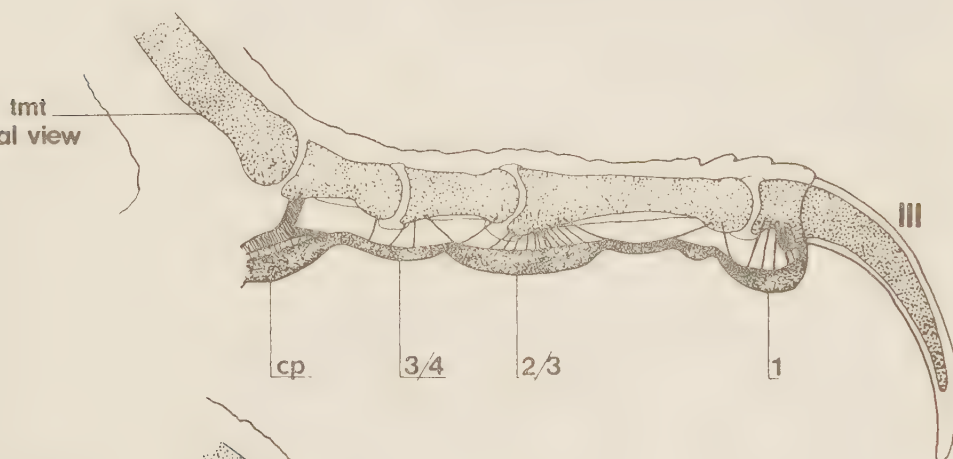


Fig. 9. (A) Diagram of transversal section through the third digit and pad III:2/3 in *Asio otus*. The bundles of collagenous fibres that attach the skin directly to the skeletal elements are indicated by lines. The pad has the plantar type of epidermis: stratum germinativum is indicated black and stratum corneum by dots. The thin epidermis at medial, dorsal, and lateral sides of the digit is shown by a line. (B) Diagram of two papillae in *Asio otus*. The orientation of the horny cells is indicated by lines in the stratum corneum. For abbreviations, see p. 74.

Medial view



Lateral view



Lateral view

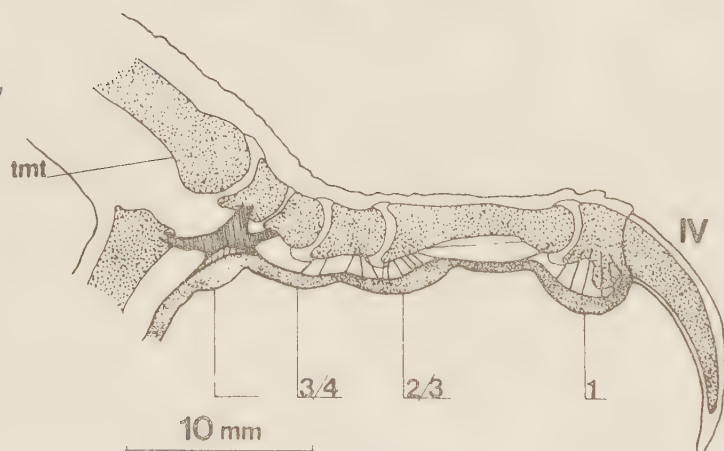


Fig. 10. Diagrams of the right foot in *Asio otus*, showing the bundles of collagenous fibres (lines) that attach the skin (dense spots) to the phalanges (spots) and to joint capsules or tendon sheaths (thin lines). For abbreviations, see p. 74.

VII. Comparative morphology of pads and folds.

ABSTRACT

Pads and folds in species representatives of 16 bird orders are surveyed. The columbiform, galliform, charadriiform, and certain coraciiform birds have a pattern with pads both at the joints and the phalanges. The joint pads are large in birds walking on hard substrate, and they fuse in extreme runners such as sandgrouses and ostrich. The joint pads are also well developed in the falconiform and strigiform birds, where they have a function in the grasp of prey; the joint pads have fused in certain species. Arboreal birds such as cuculiformes and oscines have reduced the joint pads to narrow folds. From a comparative morphological point of view, it is concluded that the pattern with joint and phalanx pads is a basic avian feature. It is lost in birds using the ground as the only substrate. This supports the hypothesis that the ancestral birds, living before Archaeopteryx, were arboreal, using the digits principally to climb and perch in trees or bushes.

CONTENTS

Introduction

Material and methods

Description of species

Ardea cinerea, Grey Heron

Calidris alpina, Dunlin

Charadrius hiaticula, Great Ringed Plover

Pterocles coronatus, Coronated Sandgrouse

Syrrhaptes paradoxus, Pallas's Sandgrouse

Ardeotis kori, Kori Bustard

Struthio camelus, Ostrich

Columba palumbus, Wood Pigeon

Treron australis, Green Pigeon

Coracias garrulus, European Roller

Merops apiaster, Bee-eater

Colius macrourus, Blue-naped Mousebird

Caprimulgus europaeus, European Nightjar

Buteo buteo, Common Bustard

Accipiter nisus, Sparrow Hawk

Falco tinnunculus, Kestrel

Pandion haliaetus, Osprey

Functional interpretations

Discussion

Literature

INTRODUCTION

Only fragmentary descriptions of pads and folds in the plantar surface of birds are given in the literature and I am not aware of any investigation devoted particularly to this subject. Heilmann (1926, p. 178) studied the pads in birds of different orders and pictured some of them. He found that the rook has one pad under each phalanx; the swan, on the contrary, has one pad under each joint; the stork has a combination, i.e. pads under both the phalanges and the joints. He also noticed the occurrence of individual variation in pattern of pads. Heilmann's observations were ignored, and many drawings of birds in the literature are vague concerning the pads.

In earlier studies (p. 6, 21, 54, 62), I described the plantar surface in domestic hen, passerines, woodpeckers, cuckoos, parrots, and owls. The present study describes seventeen species, representing ten other bird orders, living in trees or on dry or wet ground. The swimming and diving birds are excluded as they have reduced pads - many extremely water adapted birds lack pads and furrows - and as they are usually considered to be derived from terrestrial birds (Storer 1960). Heilmann's distinction between phalanx pads and joint pads is maintained. The pattern of pads is compared with what is known about the habits and the function of the foot in walking on ground or perching in trees. The basic approach in the present study is comparative morphological, and the evolution of pads in birds from this point of view is discussed.

MATERIAL, METHODS, AND TERMINOLOGY

Table 1 shows the seventeen species and number of investigated birds; they are classified in ten orders according to Storer (1971). The individual variation was examined in Charadrius hiaticula, Calidris alpina, and Columba palumbus. As the individual variation in domestic hen and seven passerine species has been described and discussed in earlier chapters (p. 9, 24), this subject is not particularly treated in the present study.

Coracias garrulus and Merops apiaster were studied in the dried skins in the zoological museum of the University of Lund whereas the other species were studied in fixed preparations or living birds. Struthio camelus and Ardeotis kori were supplied from the Institute of Comparative Anatomy at the University of Copenhagen,

the birds having lived in the zoological garden; the two pigeons Treron australis were cage birds.

The feet, except those of the skins, were fixed in a mixture of 80 per cent alcohol, concentrated formol, and concentrated acetic acid (18:1:1). Some feet were decalcified in 5 per cent nitric acid. The whole digits or part of them were embedded in celloidin, cut at 40 or 60 μ m on a sleigh microtome, and stained with Ehrlich's haematoxyline for the study of pads, papillae, and furrows.

The plantar surface consists of pads, in certain species also folds, being separated by furrows. In the diagrams, lines indicate the pads and folds. The spaces between the pads and folds show the furrows. A furrow is recognized when the papillae are separated by a gap, which is opened and closed when the digit is bent. In certain birds, i.e. Charadrius hiaticula and Caprimulgus europaeus, the furrows are shallow and the pads lie close together; in the diagram, the pads are therefore drawn close together.

The position of pads and folds was determined in relation to the phalanges and joints. In the fixed material, the phalanges and joints were localized by dissection; in the living birds, by bending and stretching the digits.

The pads and folds are designated according to the adjacent phalanx or joint between phalanges, as described in the study of the chick embryo (p. 9). All figures show the left foot from below; the second digit is to the left and the fourth digit to the right.

DESCRIPTION OF SPECIES

Ardea cinerea (Fig. 1)

The foot has long and slender digits. Digit I and II oppose. They are probably the most important part of the foot in the grasp of branches. The proximal part of digit III and IV are connected by skin.

The furrows are distinct and the pattern of pad is simple. There is one small pad at each joint and one large pad at each phalanx. Pad IV:4/5 is comparatively large. The central pad is divided into two parts. Pad I:2 is divided into one large proximal pad and one small distal pad.

Calidris alpina (Fig. 2)

The digits are long and slender; digit I is short and displaced proximally.

There is one pad at each joint and one pad at each phalanx. Pad II:3, III:4, and IV:5 are subdivided in 30, 70, and 25 per cent of the examined birds, respectively; pad II:2/3 and III:3/4, in 90 and 50 per cent, respectively. The central pad is

comparatively large and extends to the proximal parts of the anterior digits.

Charadrius hiaticula (Fig. 2)

Digit I is lacking. The anterior digits are short compared with the body. In each digit, the proximal phalanx is the longest. The basal part of digit III and IV are connected by skin.

The furrows are shallow and the pads lie close together, causing a substantial individual variation in the occurrence of furrows, which affect the size of pads.

There is one pad at each phalanx and one pad at each joint. Pad II:1/2 and II:2 fuse in 30 per cent. Pad II:3 is always subdivided into two pads, but the distal pad II:3 is further subdivided in 90 per cent.

Pad III:1/2 and III:2 fuse in 90 per cent; pad III:2 and III:2/3, in 35 per cent. The pattern in the diagram of Fig. C occurs only in 10 per cent of the examined birds. Pad III:3 is lacking in about 10 per cent, when there is only one furrow at the middle of phalanx III:3. Pad III:4 is further subdivided in 50 per cent. Pad III:4 in the diagram is shown as two pads, but the variation of types, from one to four pads, is substantial and includes variation in the size of the central pad.

Pad IV:2 and IV:2/3 are fused in all the examined birds. Pad IV:3 is lacking in 50 per cent and pad IV:4 in 30 per cent. Pad IV:5 is subdivided into two or three pads.

Ardeotis kori (Fig. 3)

Digit I is lacking. Digit III is substantially longer than digit II and IV. Phalanx III:2, IV:2, and IV:4 are reduced in length, whereas the proximal phalanges, II:3, III:4, and IV:5, are long and held in an anteroventral position.

The plantar surface has four pads, one in each of the three digits and one in the central foot. The papillae are densely packed in the pads, forming a smooth surface, but spaced out between the pads and then in structure resembling those on the sides of the digit. In the central foot, a thick dermal layer and a large subarticular cartilage for trochlea III elevate the tarsometatarsus and keep the proximal phalanges in an obliquely downwards position when the bird is resting. The pad in digit III and that in digit IV are flexible in particular regions without any furrows, which is indicated by broken lines in the diagram.

Pterocles coronatus (Fig. 3)

Digit I is rudimentary and separated from the central foot. Digit IV has only four phalanges. In each of the digits, the proximal phalanx is long. The proximal parts of the anterior digits are connected by skin.

The pads of the anterior digits have fused: there is one large pad in digit II, two large and one small pad in digit III, and one large pad in digit IV; the central foot has one large pad. The distal pads in the anterior digits are flexible without furrows in certain regions, indicated by broken lines in the diagram.

Syrrhaptus paradoxus (Fig. 3)

Digit I is lacking and digit IV has only four phalanges. The digits are kept almost parallel; digit II and IV are substantially shorter than digit III. Phalanx II:2, III:2, and IV:2, are rudimentary and joint II:1/2, III:1/2, and IV:1/2 are immovable.

The plantar skin is unique among birds (Reichenow 1913:263, von Boetticher 1930) in that the digits have fused and the skin forms one single plate, which extends proximally to the tarsometatarsus, forming a heel to walk on. The digits and the sole are easily bent upward above the horizontal plane, but it is difficult or impossible to bend it downward below the plane. This is related to the lack of furrows and the structure of the joints.

Struthio camelus (Fig. 3)

The Struthio camelus has only two digits, III and IV, but the number of phalanges is the same as in most other birds, four and five, respectively. Digit III is furnished with a heavy claw, whereas digit IV mostly lacks a claw or has a rudimentary one (Forbes 1882).

The plantar surface of the foot has two pads: one ventral to phalanx III:1, III:2, and III:3 and one ventral to phalanx IV:1, IV:2, IV:3, and IV:4. These pads have high and densely packed papillae which form a smooth surface. The skin at phalanx III:4 and IV:5 has the papillae separated from each other, their morphology being similar to the papillae at the sides of the digits.

The morphology of the digits and pads is related to the way of standing, walking, and running. In the standing, phalanx III:4 is held obliquely downwards. The phalanx has a prominent head with an extensive articular surface. Joint III:3/4 functions as a heel. Digit IV is often held above the ground; for it to contact the ground, phalanx III:4 has to be somewhat lowered. This means that only digit III is used when walking and running and digit III and IV when standing; digit IV adds to the digit movements that balance the body over the small area covered by the feet.

The insertion of the tendons of flexor muscles and the attachment of the pads to the skeletal elements show differences in the two digits, which are also related to the differences in function. The tendon of M. flexor digitorum longus has a tiny branch to digit IV where it inserts on the rudimentary phalanx IV:1;

the main tendon branch goes to digit III and inserts on the base of phalanx III:1. This means that the principle function of *M. flexor digitorum longus* concerns the flexion of digit III, and that digit III and IV are moved almost independently. The tendon of *M. flexor perforatus digiti IV* inserts by the principle branch on the base of phalanx IV:4 whereas the branches to phalanx IV:3 and IV:4 have fused with the ventromedial and ventrolateral surface of phalanx IV:4. The tendon spreads and makes an extensive fibrous contact with the deep surface of the pad at phalanx IV:3 and IV:4. The tendon of *M. flexor perforans et perforatus digiti III* and *M. flexor perforatus digiti III* run in tendon sheaths and insert on the phalanges in the same way as in most other birds. The pad in digit III is intimately and strongly connected to the phalanges and tendon sheaths by heavy bundles of collagenous fibres, but not to the tendons before their areas of insertion. Thus, digit III has three flexor muscles with tendons free movable in tendon sheaths, whereas digit IV has only one functionally important flexor muscle that has fused both with two phalanges and with the pad.

Columba palumbus (Fig. 4)

Digit I has three pads, interpreted as phalanx pads. The distal pad I:2 lies at the distal part of phalanx I:2, but it may alternatively be interpreted as a displaced joint pad, I:1/2.

The central pad is large and extends ventral to phalanx III:4. Pad II:3 is notably large.

Pad II:2 is subdivided in 25 per cent; pad III:2, in 35 per cent; and pad III:3, in 5 per cent. Pad IV:3 is present only in 8 per cent.

Treron australis (Fig. 4)

The feet of *Treron australis* are smaller than those of *Columba palumbus*. The pattern of pads differs in certain respects. There is a pad at each of joint I:1/2, II:1/2, III:1/2, and IV:1/2. Pad II:2/3, III:2/3, III:3/4, and IV:4/5 are comparatively small. The pads in digit III are similar in the two pigeons, whereas there are more pads in digit IV of *Treron australis*, namely pad IV:3 and IV:4, being only occasionally or never present in *Columba palumbus*.

Coracias garrulus (Fig. 4)

The digits are free movable to each other. The skin is comparatively thin. Digit I is directed posteriorly and pad I:2 is large. Digit II has pad II:2 subdivided, and the parts have the same size as pad II:1/2. Pad II:2/3 lies at the proximal part of the pad, somewhat displaced. Digit III has one pad at each phalanx and one pad at each joint; pad III:2/3 and III:3/4 are also somewhat displaced in relation

to the respective joints. Digit IV has one pad at each phalanx and one pad at each joint.

Merops apiaster (Fig. 4)

The foot is syndactyle; the anterior digits are connected from the base to point II:2/3, III:2/3, and IV:2/3, only the distal two phalanges of the three digits being free.

Digit I is directed posteriorly and pad I:2 has a broad base. Pad II:2, III:2, and IV:2 are subdivided. There is probably an individual variation in this subdivision.

The four pads designated A, B, C, and D in the diagram are interpreted as fusions of two or several pads. Pad A consists of pad III:2/3 and IV:2/3; pad B of pad III:3 and IV:3; pad C of pad II:2/3, III:3/4, and IV:4; pad D of pad II:3, III:4, IV:4/5 and IV:5.

Colius macrourus (Fig. 5)

Digit I is directed medially but the digit can rotate anteriorly; digit IV can rotate laterally or even posterolaterally. Thus, the digits may be directed anteriorly in a pamprodactyle griff or they may diverge so that digit I and IV oppose, grasping against each other. Phalanx IV:3 is shorter than phalanx IV:2 and IV:4, meaning a reduced length of the phalanx in the middle of the digit.

There is one fold at each of joint I:1/2, II:1/2, III:1/2, and IV:1/2. Digit II and III have one pad at each joint and one pad at each phalanx, but digit IV has pads only at the phalanges.

The central pad is divided into two parts.

The posterior side of the tarsus is furnished with papillae, having the same structure as those in the sole. At the distal part of the tarsus, the skin is thickened to a pad, separated from the central pad by a furrow; this pad is not shown in the diagram. A similar pad lies at the tarsal joint.

Caprimulgus europaeus (Fig. 5)

The feet are tiny in relation to the body size. Digit III is long and furnished with a great comb on the medial side. Digit IV is comparatively short and has only four phalanges; it is not known which of the five phalanges is lacking; they are tentatively numbered from 1 to 4.

The proximal part of the anterior digits are connected by skin. The skin in the sole is thin and the papillae are large and flat. The furrows are shallow and the individual variation is probably substantial. The diagram shows the pattern of pads as I observed it in two specimens.

Digit I has no furrow. The other three digits have pads at the phalanges and at the joints. Pad II:3, III:4, and IV:4 are subdivided. The central pad is divided by one or two furrows. There is no pad at joint II:1/2, III:1/2, and IV:1/2.

Buteo buteo (Fig. 6)

The digits are comparatively thick, which is correlated with the heavy body. Digit I and II are strongest. Phalanx IV:3 and IV:4 in the middle of digit IV are short, and phalanx III:3 is shortest in digit III.

Most of the papillae are free from each other but some are connected to a small extent at their bases. The dermis consists of densely packed collagenous fibres. The structure is thus comparable to that described in the owls (p. 70). The pads are separated by furrows, but the flexibility often includes the skin with papillae adjacent to the furrow. It is uncertain whether these furrows develop in the same way as the furrows in the domestic hen (p. 10). The diagram shows the pattern of pads as I observed it in three specimens, but there may be a considerable individual variation.

Pad III:2 is subdivided into two pads in one of the specimens; one specimen has a small pad at joint II:1/2. Similar variation was observed in pad IV:2. It is impossible in the examined material to determine whether there is a particular pad at joint II:1/2, III:1/2, and IV:1/2, or if the pad when present is a separated part of the phalanx pad.

Pad IV:4/5 and IV:5 are fused in one individual and pad IV:3/4 and IV:4/5 in another. Pad I:1, proximal pad I:2, pad II:1, II:2/3, III:1, III:2/3, IV:1, and IV:2/3 are prominent pads.

Accipiter nisus (Fig. 6)

The digits are slender and digit III is particularly long. Phalanx II:3 is short, and digit II is about half the length of digit III. Digit I and II oppose.

The plantar surface is described by Blaszyk (1935). The structure of the papillae and the deep dermis in Accipiter nisus is comparable to that in Buteo buteo: the dermis is dense and the papillae are free from each other.

The following pads protrude substantially: pad III:1, III:2/3, IV:1, IV:2/3. These pads have an inner core of subcutaneous tissue; this tissue is surrounded by a dense, ligamentous layer of collagenous fibres, and this layer is intimately connected to the phalanges at the joint. Pad III:2/3 is assymetric, and the protruded top is directed anteroventrally.

Falco tinnunculus (Fig. 7)

Digit I is comparatively short, but the claw is larger than those of the anterior

digits. Phalanx III:3, IV:3, IV:4, and IV:5 are short.

Falco tinnunculus has the same structure of furrows and papillae as Buteo buteo.

Pad I:1, II:1, II:2/3, III:1, III:2/3, IV:1, IV:2/3, and central pad protrude from the plantar surface. Pad II:2 and IV:2 are subdivided in the studied bird, as might probably occur also in pad I:2 and III:2 in other birds.

Pandion haliaetus (Fig. 7)

Digit I and IV are highly movable sideways. Digit IV may rotate backwards and the foot perform a griff, with digit II and III pointing anteromedially and digit I and IV posterolaterally. Also a griff with digit III and IV pointing anterolaterally and digit I and II posteromedially is possible. The claws are heavy and of equal length.

Phalanx III:3, IV:3, and IV:4 are short. The principle articulation in digit IV occurs in joint IV:2/3, to a lesser extent in joint IV:4/5, whereas joint IV:3/4 is almost immovable.

The papillae are free from each other and are pointed. The stratum corneum in the papillae is similar to that in the scale. The flexibility in the plantar skin lies in the stratum corneum between the papillae. The skin has a dermis with densely packed collagenous fibres. The structural element in the pad is the dermis, and the pointed papillae aid in the holding of slippery fishes. Similar adaptations in the papillae occur in the fish-eating owls (Meise 1933). The structure of the furrows is comparable to that in Buteo buteo.

The scales on the sides of the digit are small and the attachment of the skin to the skeletal element is direct (p. 62).

There is a large pad at joint IV:2/3, IV:3/4, IV:4/5, and IV:5 which has fused with skin in the proximal part of digit III; the pad is designated pad B in the diagram. The pad at phalanx II:3 has fused with skin at the proximal part phalanx III:4; this pad is designated pad A in the diagram. Pad I:1, II:1, II:2/3, III:1, III:2/3, III:3/4, IV:1, A and B are large.

FUNCTIONAL INTERPRETATIONS

Much is known about the morphology of the leg muscles, their areas of origin and insertion; the extensive literature has been reviewed by Hudson (1937) and George & Berger (1966).

The muscles that operate the digits have their bellies at tibiotarsus or tarsometatarsus. The flexor muscles are the largest of the digit muscles and the most important in walk and perch. The bellies of the flexor muscles, except M. flexor

hallucis brevis, lie at the tibiotarsus. Their tendons of insertion pass the tibial cartilage at the intertarsal joint, the subarticular cartilages at the trochleas, and the tendon sheaths ventral to the phalanges before they insert on the phalanges. The tibial and subarticular cartilages function as pulleys for the tendons. The tendon sheaths in certain regions are supplied with ridges which interlock with ridges on the ventral side of certain tendons, the "Sperrvorrichtung" of Schaffer (1903). Bock (1968) discussed the mechanism of one- and two-joint muscles, but his study is restricted to those muscles whose forces lie on a single vector line that connect the point of origin and insertion; the flexor muscles of the digits are more complicated. Certain of the flexor muscles also interact by the connexion of their bellies or the connexion of their tendons by tendon vincula.

I do not know of any study devoted to the action of the digit muscles as forces and the phalanges as levers in the grasp of branches or for walking on ground. Cracraft (1971) made a careful study of the leg in the domestic pigeon and described the movements of the leg during the walking cycle, but he did not analyse the movements of the digits. Goslow (1972) measured the outforces of the talons in various raptors that were due to contraction in the long flexor muscles. The studies by Miller (1937) on Hawaiian Goose, by Fischer (1946) on New World vultures, by Berger (1952) on cuckoos, by Owre (1967) on anthinga and cormorants, by Klemm (1969) on procellariiform birds, and by Raikow (1970) on stiff-tailed ducks, Oxyurini, have their basic approach in the comparative morphology of muscles and skeleton, and they infer the adaptations principally from differences in morphology in related species with known general differences in the habits of walking, swimming, diving, or perching.

The information on how the digits and the pads are used in grasping branches or in walking on ground in various birds is restricted to the general knowledge on birds behaviour. The following functional interpretations are deduced from the morphology of pads in birds with substantial differences in the habits of running, walking, and perching. First, the birds with terrestrial habits will be discussed.

The heron Ardea cinerea and the sandpiper Calidris alpina are wading birds, walking slowly on wet and soft ground; Ardea cinerea also frequents trees for rest and nesting. The digits of these species are long and narrow preventing the birds from sinking down in soft ground (Storer 1960). The long digits impede fast running. These species have small joint pads and long phalanx pads.

The plover Charadrius hiaticula frequents shores, river banks, and other areas near water with a sparse plant vegetation. This means a harder ground than the sandpiper. The proximal phalanx in the anterior digits is long and the distal phalanges comparatively short. This is a characteristic feature of running animals. Charadrius hiaticula has the joint and phalanx pads of about equal size. Equal size

of joint and phalanx pads also occurs in the smaller bustard species Otis tetrax and Otis tarda, examined in skins.

The kori bustard, Ardeotis kori, is among the heaviest of recent flying birds; it lives on grassy and bushy plains. It is a fast runner. Digit III is substantially longer than digit II and IV. The proximal phalanges are comparatively long and held obliquely downwards. These two features are adaptations for running. Ardeotis kori has only four pads, one in the central foot and one in the distal part of each digit.

The sandgrouses Pterocles coronatus and Syrrhaptes paradoxus live in arid and open areas with sparse or no plant vegetation. They can run fast. Both species have digit III substantially longer than digit II and IV. Pterocles coronatus has one pad in the central foot and one large pad in the distal part of the digits, the pattern being analogous to that in Ardeotis kori. Syrrhaptes paradoxus has the whole plantar surface developed as one plate. The digits cannot be moved independently, and the foot in Syrrhaptes paradoxus is more specialized for running than the foot in Pterocles coronatus.

The ostrich Struthio camelus lives in waste areas, semi-deserts, and open grasslands. It occurs in a continental region where there has been advanced carnivore mammals for a long time (Romer 1966); it is the most advanced runner among the ratites. The foot has only two digits which may be moved independently; only digit III is used in the run. The Struthio camelus has one pad in the distal part of each digit.

The mentioned terrestrial species occur on various substrates, from soft and wet to dry and hard. On hard substrate, the species have greater joint pads than on soft. With increased body size or increased running capacity, the pads fuse and the distinction between joint and phalanx pads disappears. This suggests that the joint pads have a function in the walk. The skeletal adaptations for a fast run are: elongation of the basal phalanges; shortening of the distal phalanges; long digit III and short digit II and IV; elevation of the proximal phalanges. The concomitant adaptations in the skin are fusions of pads.

Arboreal habits occur in species of different orders, although in many, they are combined with terrestrial habits.

The passeriformes comprise more than half the number of species of known birds. They have small bodies compared with birds of most other orders. The small body and the small feet with a long and opposable digit I has probably been an important factor for the radiation of the order and the exploration of habitats with slender branches and thin twigs in trees and bushes. A number of European passerines were examined (p. 21), and a basic pattern of pads is recognized. There are twelve phalanx pads and one pad in the central foot. The joints have small structures,

designated folds, but the folds may be lacking. The development of phalanx pads and the reduction of joint pads to folds (p. 34) facilitate a bending of the digits around thin twigs (Fig. III:3). The pattern of pads in species living on ground or tree trunks changes, and the basic pattern of pads disappears. In Alauda arvensis, there are small pads at the joints; it is not known whether these pads are enlarged folds or displaced phalanx pads, but it shows that the occurrence of pads at the joints is a feature in birds with terrestrial habits. This supports the hypothesis that the basic pattern in the passerine species with twelve phalanx pads is an adaptation to thin branches or twigs.

The wryneck Jynx torquilla and some woodpeckers in the family Picidae are described in a previous chapter (p. 56). They are arboreal, and the woodpeckers show adaptations for tree trunk climbing. The feet are zygodactyle. The basic pattern is pads at the phalanges and small pads or folds at the joints. This means that the species of Picidae conform to the passeriform species in the development of phalanx pads.

The cuckoo Cuculus canorus (p. 57) has a zygodactyle foot adapted to grasp branches. Digit I and II are short and fit to grasp thin twigs, whereas digit III and IV are long and fit to grasp thick twigs. There are pads at the phalanges and folds at the joints. All species of family Cuculidae have zygodactyle feet, which indicates that the family is basically arboreal, although some species are terrestrial. If the pattern with pads at the phalanges and folds at the joints is a feature for the family - only one species has been examined - the development of phalanx pads can be correlated with the arboreal habits, conforming with the circumstances in the Passeriformes.

The Passeriformes, Picidae, and Cuculidae have large scales on the dorsal side of the digit, which mean a good indirect attachment of the pads to the skeletal elements (p. 62).

The parrots, family Psittacidae, are with few exceptions arboreal species. They differ from the above-discussed species in their sluggish way of moving on twigs and their climbing with the feet and beak in co-operation. The pattern of pads is basically different (p. 57). The phalanx pads are large and many of them subdivided by furrows at the joint, which facilitate the bending of the digit. The pattern of pads in Psittacidae is related to the direct attachment of the skin to the skeletal elements and to the sensory function of the papillae.

The mousebirds, family Coliidae, are arboreal species that can perch on twigs or climb on vertical surfaces. Digit I and IV may change direction so that they either are directed medially and laterally to oppose in the grasp of twigs or are directed anteriorly in order to climb on vertical surfaces. Only one species was studied. Digit II and III has both joint and phalanx pads, whereas digit IV has

only phalanx pads. The lack of phalanx pads or folds in digit IV is clearly related to the more intense bending of this digit in the grasp of twigs.

Certain other of the studied species are completely or partially arboreal. The roller Coracias garrulus frequents trees, but it searches for much of its food on the ground. There are both phalanx pads and joint pads in the digits, although the joint pads seem to be somewhat displaced in relation to the joints. The bee-eater Merops apiaster is insectivorous; it rests in trees and preys in the air. The foot is syndactyle. There are five large pads which are interpreted as fusion of various phalanx and joint pads. There are many species of pigeons, family Columbidae, and most species are at least partially arboreal. The examined species have both phalanx and joint pads. The domestic fowl has both joint and phalanx pads. When frequenting trees, these mentioned species probably use comparatively thick twigs or branches: thick in relation to the span of the digits. This means that the digits are not so intensely bent as in the Passeriformes and Cuculiformes.

The nightjar Caprimulgus europaeus catches prey flying in the air. The feet are used only to stand or walk slowly. It is notable that digit III is substantially longer than digit II and IV, which is a feature of running birds (cf. Ardeotis kori and Syrhaptes paradoxus); digit IV has a reduced number of phalanges. The plantar skin is thin and there is probably a substantial variation in the occurrence of furrows, but the pads are interpreted as joint and phalanx pads.

The species of the families Accipitridae, Falconidae, Pandionidae, and Strigidae (p. 62) sit on branches to rest or watch for prey. The feet are also used to grasp prey. Some of the species have reduced length of certain phalanges. The variation in the structure of the feet and in the pattern of pads indicates differences in the function. The long digit III and short digit II in Accipiter nisus does not occur in the other examined species. The osprey Pandion haliaetus and the owl Asio otus are comparable in the high sideways movability of digit I, II, and IV; they have some large pads which are interpreted as fused pads.

The analysis of the arboreal or partly arboreal species may be summarized in the following way. The species of Passeriformes, Picidae, and Cuculidae have reduced the joint pads to folds; certain folds are lacking and are replaced by furrows. The species of Coliidae has furrows at the joints in digit IV. This pattern is related to an intense bending of the digits around twigs with diameter substantially less than the span of the digits. The two anterior digits in the examined species of Psittacidae have furrows at the joints which are also related to the bending of the digits, but these furrows subdivide joint pads. Other species frequent both the trees and the ground, or they perch in trees, catching prey in the air or on ground. These species have both joint and phalanx pads. They are supposed to frequent branches that have a diameter of about the same size as the

span of the digits. The species of Falconiformes and Strigidae show adaptations in both pads and phalanges for the grasp of prey.

COMPARATIVE INTERPRETATIONS

In the present study, I have described the plantar surface in species representing eleven families: Struthionidae, Ardeidae, Pandionidae, Accipitridae, Falconidae, Otididae, Charadriidae, Scolopacidae, Pteroclididae, Columbidae, Caprimulgidae, Coliidae, Meropidae, and Coraciidae. Previous studies deal with species representatives of the families Phasianidae (p. 6), Psittacidae, Cuculidae, Picidae (p. 54), and Strigidae (p. 62). A great number of passeriform species are compared and a basic pattern of pads and folds is deduced (p. 39).

All these data suggest a basic pattern of pads in the birds. This is the theme of the study and is used in the designation of the pads. The pattern comprises one pad at each phalanx and one pad at each joint. At the distal joints, I:1/2, II:1/2, III:1/2, and IV:1/2, there may be small pads or folds, or the structures may be lacking. The central pad is not comparable in all the different families; it has a different position in relation to the tarsometatarsus and metatarsus I. The basic pattern is therefore restricted to the phalanges.

The basic pattern occurs in Ardeidae, Scolopacidae, Charadriidae, Columbidae, Phasianidae, Caprimulgidae (although one phalanx is lacking in digit IV), and Coraciidae.

The species of Passeriformes, Picidae, and Cuculidae have the joint pads reduced to folds or the structures at the joints are lacking, being replaced with a single furrow.

The species of Coliidae has the basic pattern in digit II and III, but has changed the pattern in digit IV by reduction or fusion of pads so that there are furrows at the joints. The species of Meropidae has a syndactyle foot; two or several joint or phalanx pads have fused.

The species of Falconiformes and Strigidae have less well-defined furrows, but many joint pads are elevated. Certain pads have fused in the Pandionidae and Strigidae.

DISCUSSION

From comparative morphological points of view, a basic pattern of pads in birds is deduced, meaning one pad at each phalanx and one pad at each joint; the pad in the central foot is not comparable in all birds. The reduction of joint pads to

folds in certain arboreal species is related to the function of grasping branches or twigs which are thinner than the span of the digits. The adaptation for running on hard substrate is enlargement of joint pads and fusion of several pads so that the basic pattern disappears.

The question may be posed whether this basic pattern can be attributed to any known fossil record on the avian line of evolution.

The origin of birds is fragmentarily known as concerns the fossil records. The skeleton and feathers of Archaeopteryx in the Upper Jurassic is well known (DeBeer 1954). The feet of Archaeopteryx had a comparatively short but opposable digit I; digit III was longer than digit II and IV; and the ungual phalanges were supplied with claws. Metatarsus II, III, and IV were elongated and had, at least in the proximal parts, fused to each other and to the distal tarsals, forming a tarsometatarsus. Metatarsus I was small and placed at the distal part of tarsometatarsus.

The structure of digits and metatarsals is rather similar to that in modern birds. Superficially, the hind leg reminds of that in Columbiformes, Galliformes, or certain Falconiformes. The proportions have been compared with the curassows among recent birds. The study of Steinbacher (1935) on the internal anatomy of the feet of Psittacidae, Cuculidae, Galbulidae, Picidae, Trogonidae, and Coliidae shows differences that indicate separate evolution of at least certain of these feet. It is difficult to think that these feet have evolved from that in Archaeopteryx, which had already reduced the central foot (cf. Bock o. Miller 1959). It is more probable that the different types of feet evolved from animals that lived before Archaeopteryx or had a more primitive foot.

The nearest relatives to Archaeopteryx are usually thought to be the pseudosuchian reptiles in the Triassic (Heilmann 1926, Romer 1966, Brodkorb 1971) and particularly the Euparkeria in the Lower Triassic, recently described in detail by Ewer (1965). This reptile species showed bipedalism in that the hind legs were one and a half times as long as the fore legs. Digit III in the hind legs was longest and digit IV shorter than digit III, which is a feature also in birds. Digit I was shorter than digit II, directed anteriorly, and held close to digit II. Digit V was comparatively short and directed laterally; metatarsus V was peculiar in having a broad proximal part. The digits had sharp claws. Ewer (1965) concluded from the structure of the hind legs and the pelvic girdle that the femur was held horizontally during rest and slow walk and vertically during fast walk. The humerus was held horizontally. The erect gait evolved in the dinosaurs of the Triassic and was probably associated with a high body temperature and a continuous high level of activity (Bakker 1971).

I think it is likely that it was Euparkeria or some of its relatives in the

Triassic that had the basic pattern with joint and phalanx pads and used the digits to grasp branches or twigs. These supposed ancestors of birds may have frequented both the ground and the trees or bushes, but they could not have been fast runners or only terrestrial; otherwise, the basic pattern of pad would have disappeared and the phalanges been reduced in length. Later, when the grasping function of the digits differentiated, certain digits became opposable for a more efficient grasp of branches, twigs, or prey, and the metatarsal part of the foot was left without contact with the substrate and became elongated. This evolution would have followed different lines in the different orders.

This means that the evolution of the birds is basically associated with arboreal habits (DeBeer 1954) and that the differentiation of the birds orders occurred in the Triassic. Other opinions have also been advanced; Galton (1970) argues for a terrestrial, cursorial, stage in the evolution of the birds before they became arboreal.

LITERATURE

- Bakker, R.T. 1971. Dinosaur physiology and the origin of mammals. - *Evolution* 25:636-658
- Berger, A.J. 1952. The comparative functional morphology of the pelvic appendage in three genera of Cuculidae. - *Amer. Midland Natur.* 47:513-605.
- Blaszyk, P. 1935. Untersuchungen über die Stammesgeschichte der Vogelschuppen und Federn und über die Abhängigkeit ihrer Ausbildung am Vogelfuss von der Funktion. - *Morph. Jahrb.* 75:483-567.
- Bock, W.J. 1968. Mechanics of one- and two-joint muscles. - *Amer. Mus. Novitates* 2319:1-45.
- Bock, W.J. & Miller, W. DeW, 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. - *Amer. Mus. Novitates* 1931:1-45.
- Brodkorb, P. 1971. Origin and evolution of birds. Pp. 19-55 in Farner, D.S. & King, J.R. (eds.): *Avian Biology*, Vol. 1. Academic Press, New York & London.
- Cracraft, J. 1971. The functional morphology of the hind limb of the domestic pigeon Columba livia. - *Bull. Amer. Mus. Natur. Hist.* 144:171-268
- DeBeer, G. 1954. Archaeopteryx lithographica. A study based on the British Museum specimen. *British Museum Natur. Hist.*, London.
- Ewer, R.F. 1965. The anatomy of the thecodont reptile Euparkeria capensis Broom. - *Phil. Trans. Roy. Soc. London.*, Ser. B, 428:379-435.
- Fisher, H.I. 1946. Adaptations and comparative anatomy of the locomotor apparatus of New World vultures. - *Amer. Midland Natur.* 35:545-727.
- Forbes, W.A. 1882. On the variations from the normal structure of the foot in birds. *Ibis* 1882:386-390.

- Galton, P.M. 1970. Ornithischian dinosaurs and the origin of birds. - *Evolution* 24:448-462.
- George, J.C. & Berger, A.J. 1966. Avian myology. Academic press, New York & London.
- Goslow, G.E. 1972. Adaptive mechanisms of the raptor pelvic limb. - *Auk* 89:47-64.
- Heilmann, G. 1926. The origin of birds. H.F.G. Witherby, London.
- Hudson, G.E. 1937. Studies on the muscles of the pelvic appendages in birds. - *Amer. Midland Natur.* 18:1-108.
- Klemm, R.D. 1969. Comparative myology of the hind limb of procellariiform birds. - *Southern Illinois Univ. Monogr., Sci. Ser.*, 2:1-269.
- Meise, W. 1933. Zur Systematik der Fischeulen. - *Ornithol. Monatsber.* 41:169-173.
- Miller, A.H. 1937. Structural modifications in the Hawaiian goose (Nesochen sandvicensis): a study in adaptive evolution. - *Univ. California Publ. Zool.* 42:1-79.
- Owre, O.T. 1967. Adaptations for locomotion and feeding in the anhinga and the double-crested cormorant. - *Ornithol. Monogr.* 6:1-138.
- Raikow, R.J. 1970. Evolution of diving adaptations in the stiff-tailed ducks. - *Univ. California Publ. Zool.* 94:1-52.
- Reichenow, A. 1913. Die Vögel. Handbuch der systematischen Ornithologie. Vol. 1 F. Enke, Stuttgart
- Romer, A.S. 1966. Vertebrate Paleontology. Univ. Chicago Press, Chicago & London.
- Schaffer, J. 1903. Über die Sperrvorrichtung und den Zehen der Vögel. *Z. Wiss. Zool.* 73:377-428.
- Steinbacher, G. 1935. Funktionell-anatomische Untersuchungen an Vogelfüßen mit Wendezehen und Rückzehen. - *J. Ornithol.* 83:214-282.
- Storer, R.W. 1960. Adaptive radiation in birds. Pp. 15-55 in Marshall, A.J. (ed.): *Biology and comparative physiology of birds. Vol. 1.* Academic Press, New York & London.
- Storer, R.W. 1971. Classification of birds. Pp. 1-18 in Farner, D.S. & King, J.R. (eds.): *Avian Biology. Vol. 1.* Academic Press, New York & London.
- von Boetticher, H. 1930. Morphologische und phylogenetische Studien über die hornige Fussbekleidung der Vögel. - *Jenaische Z. Naturwiss.* 64:376-448.

Table 1. Species and number of investigated birds, classified according to Storer (1971)

Struthioniformes

Struthionidae: Struthio camelus (1)

Ciconiiformes

Ardeidae: Ardea cinera (2)

Falconiformes:

Pandionidae: Pandion haliaetus (1)

Accipitridae: Buteo buteo (3), Accipiter nisus (2)

Falconidae: Falco tinnunculus (2)

Gruiformes

Otididae: Ardeotis kori (1)

Charadriiformes

Charadriidae: Charadrius hiaticula (38)

Scolopacidae: Calidris alpina (42)

Pteroclididae: Pterocles coronatus (6), Syrhaptus paradoxus (1)

Columbiformes

Columbidae: Columba palumbus (100), Treron australis (2)

Caprimulgiformes

Caprimulgidae: Caprimulgus europaeus (2)

Coliiformes

Coliidae: Colius macrourus (1)

Coraciiformes

Meropidae: Merops apiaster (4 skins)

Coraciidae: Coracias garrulus (8 skins)

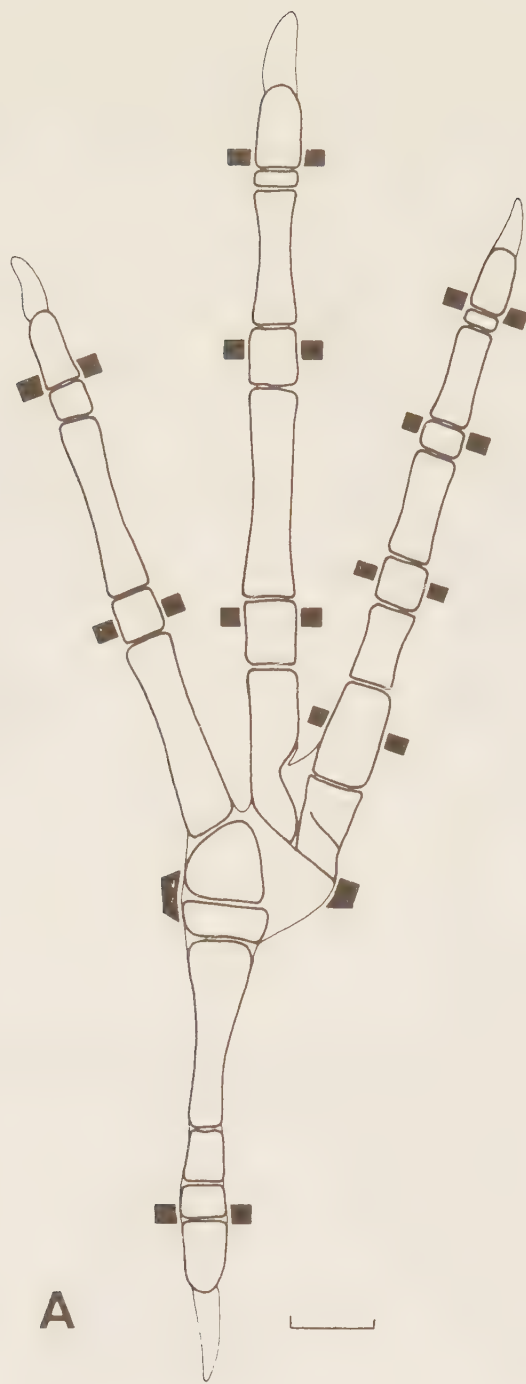


Fig. 1. Diagram of plantar surface in Ardea cinerea. Scale indicate 1 cm.

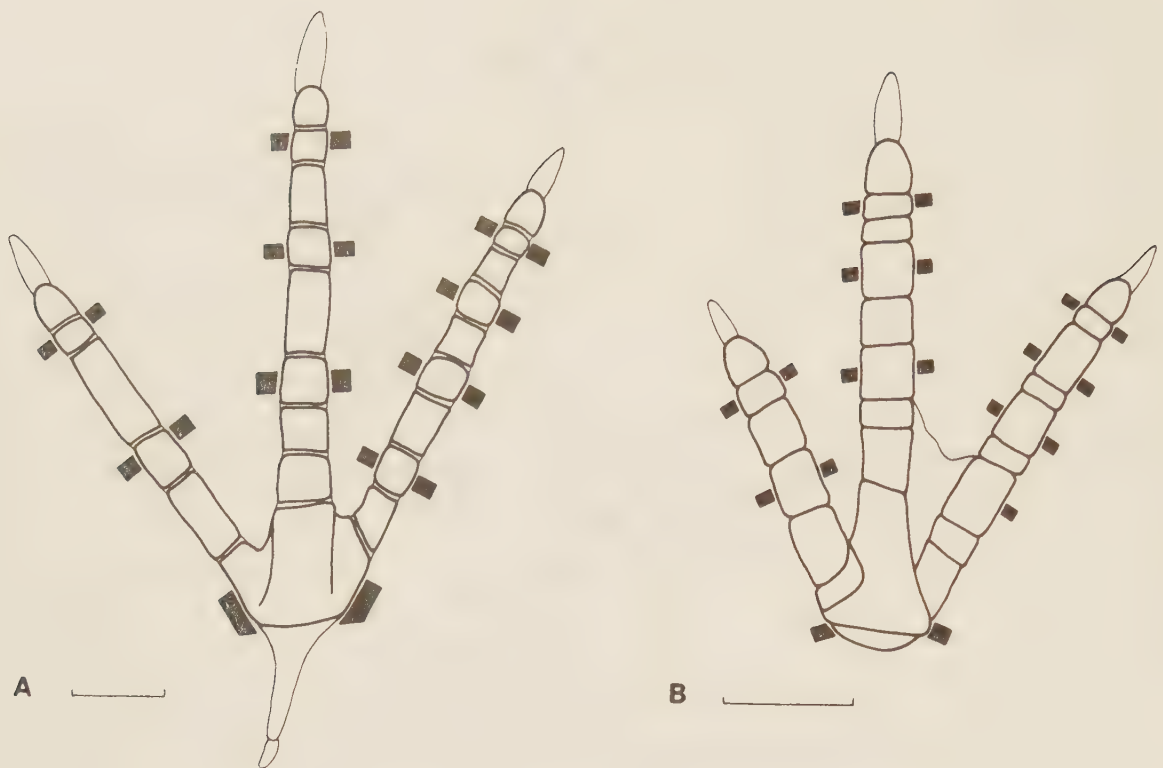


Fig. 2. Diagram of plantar surface in (A) Calidris alpina and (B) Charadrius hiaticula. Scale indicate 5 mm.

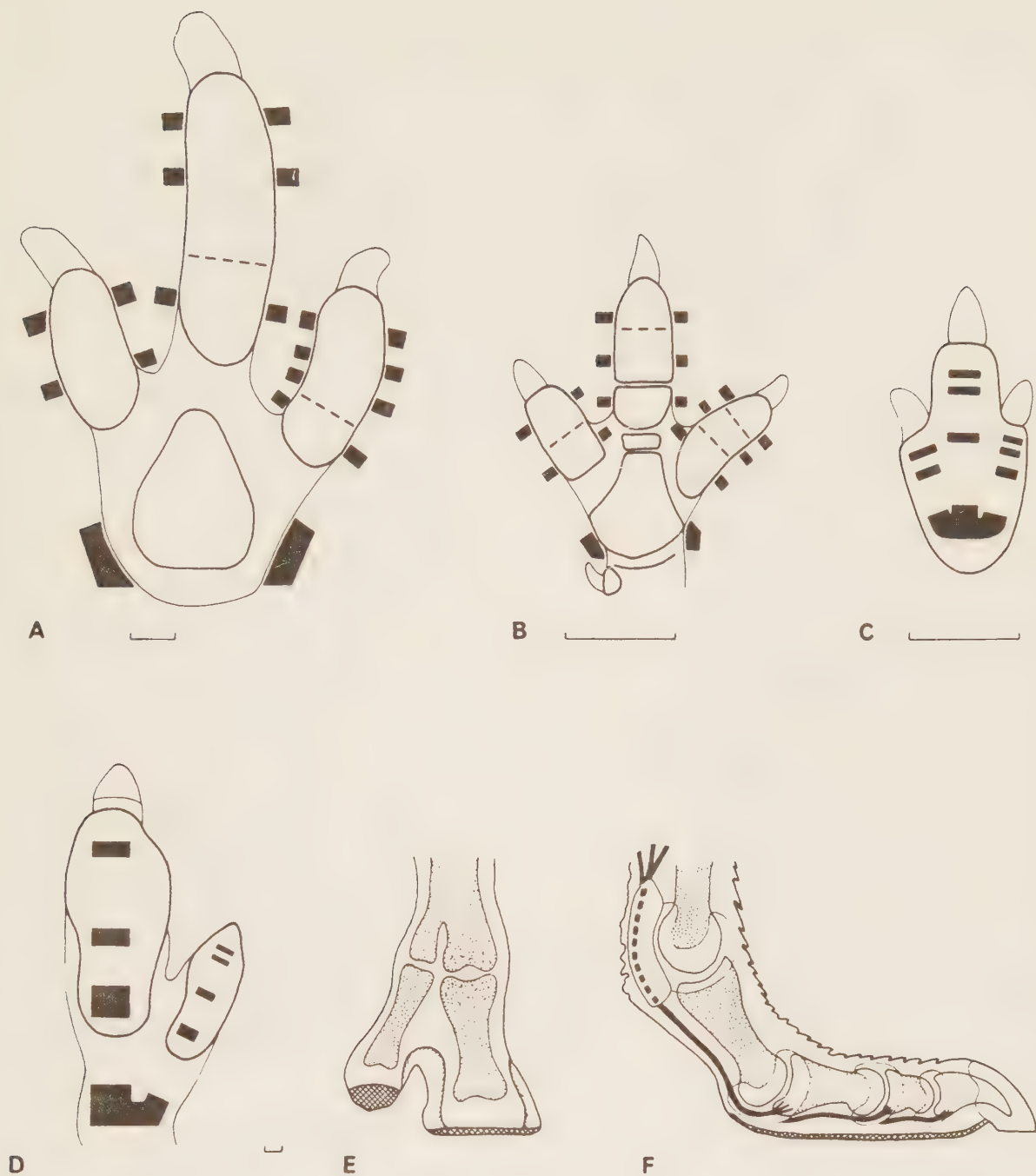


Fig. 3. Diagram of plantar surface in (A) *Ardeotis kori*, (B) *Pterocles coronatus*, (C) *Syrrhaptes paradoxus* and (D) *Struthio camelus*. (E) is a hind view and (F) a medial view of left foot of *Struthio camelus*, showing tarsometatarsus, phalanges, joint capsules, subarticular cartilage at trochlea III, and tendons of flexor muscles; the skin in the pads is indicated by crossed lines. Scale indicate 1 cm.

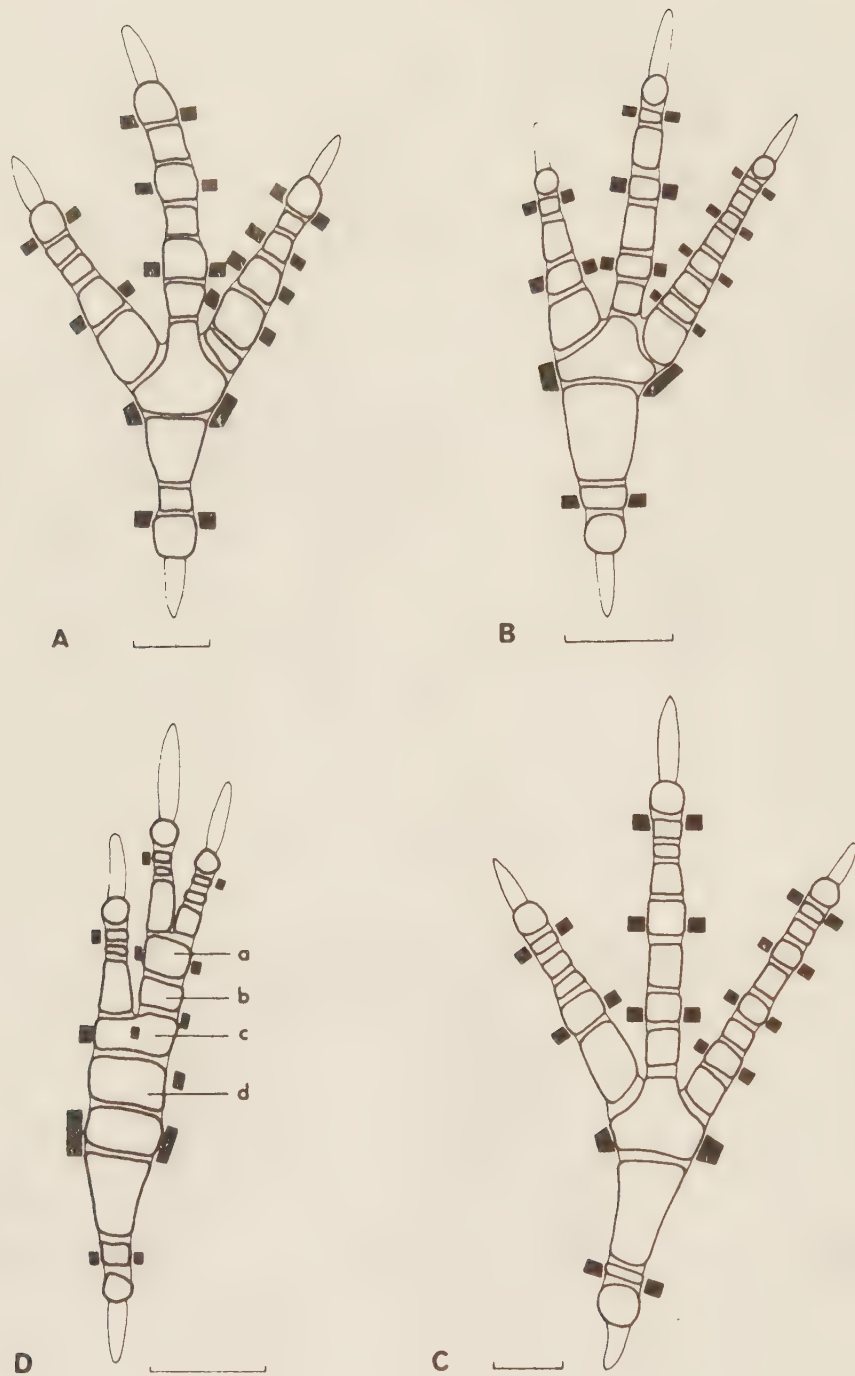


Fig. 4. Diagram of plantar surface in (A) Columba palumbus, (B) Treron australis, (C) Coracias garrulus, and (D) Merops apiaster. Scale in (A) and (B) indicate 1 cm; in (C) and (D), 5 mm.

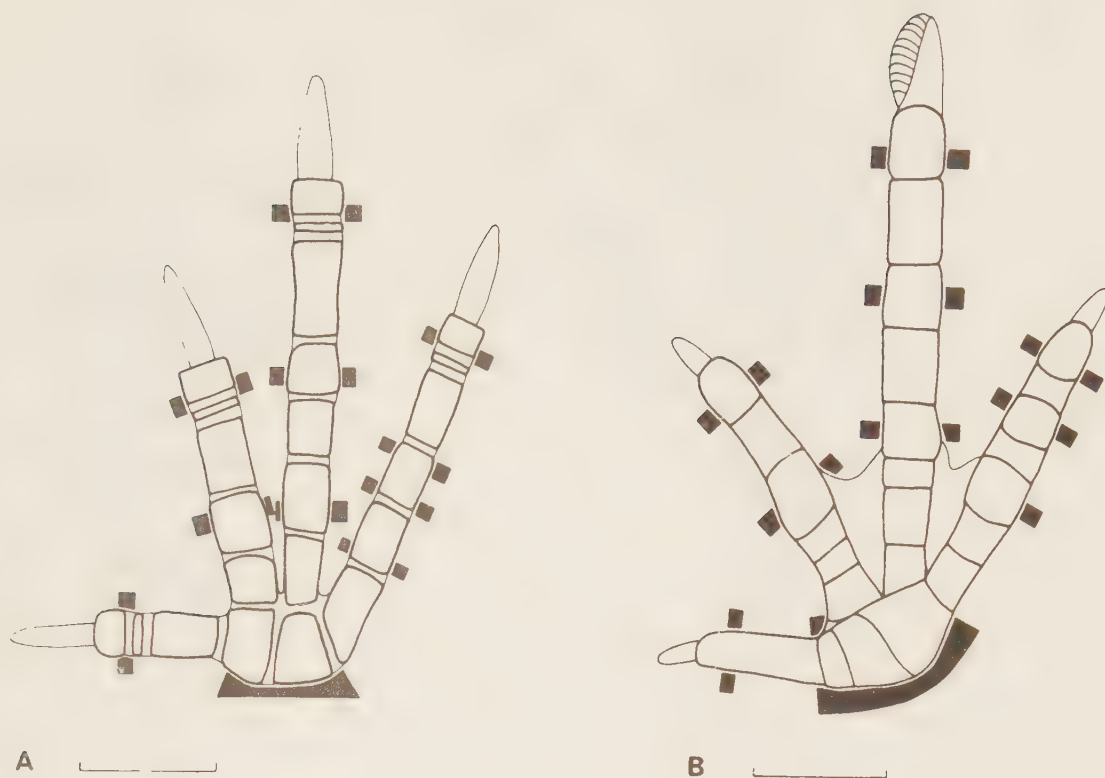


Fig. 5. Diagram of plantar surface in (A) Colius macrourus and (B) Caprimulgus europaeus. Scale indicate 5 mm.

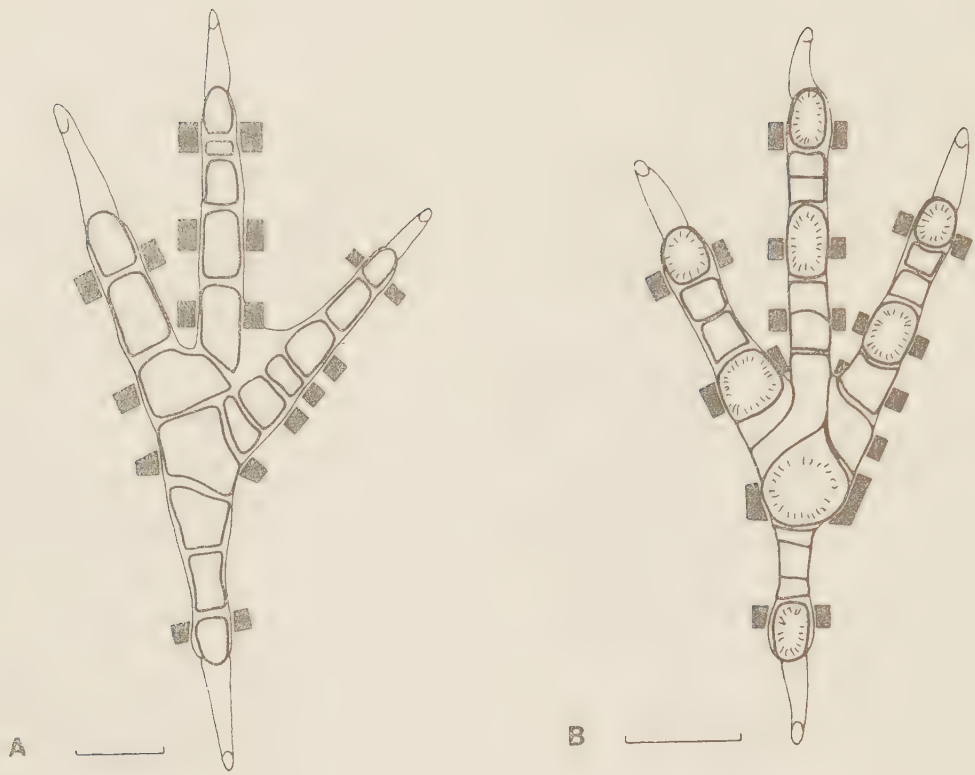


Fig. 6. Diagram of plantar surface in (A) Buteo buteo and (B) Falco tinnunculus. Scale indicate 1 cm.

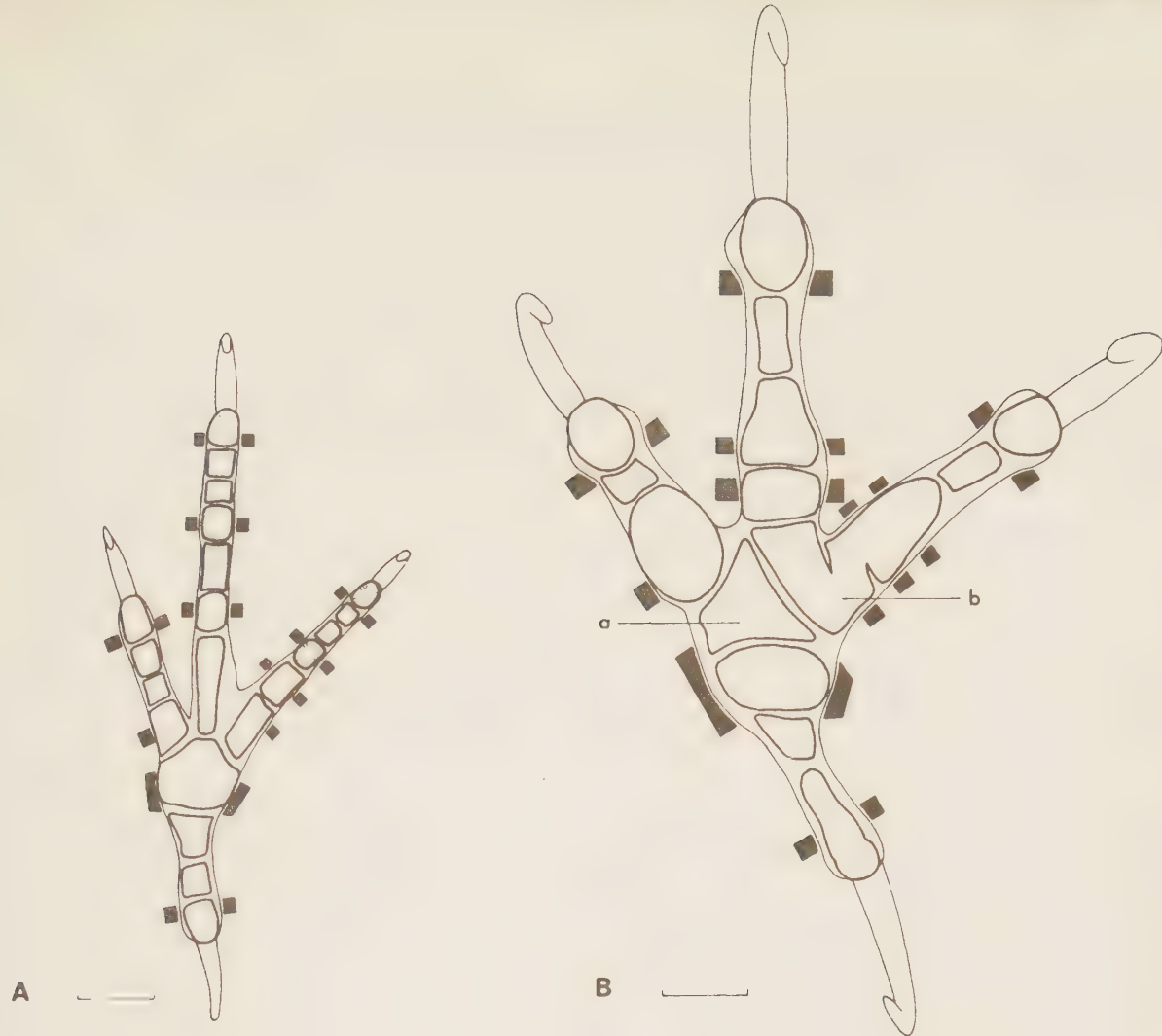


Fig. 7. Diagram of plantar surface in (A) Accipiter nisus and (B) Pandion haliaetus. Scale indicate 1 cm.

VIII. Seasonal variation in foot papillae of Wood Pigeon, Pheasant, and House Sparrow.

ABSTRACT

The horny layer, germinative layer, and secondary dermal papillae in the foot papillae were studied in histological preparations from Wood Pigeon, Pheasant, and House Sparrow.

The three species show a seasonal variation in thickness of horny and germinative layers and length of secondary dermal papillae, the highest values occurring in winter. The average values of the horny layer vary from 0.21 to 0.11 mm in the Wood Pigeon, from 0.52 to 0.22 mm in the Pheasant, and from 0.19 to 0.15 mm in the House Sparrow. The structural changes in the population extend over several months.

An analysis of correlation between the measurements in the Wood Pigeon shows that the length of secondary dermal papillae is the independent factor, and that the changes in spring are initiated by a decrease in their length. The seasonal variation is obviously an adaptation to the environmental temperature, implying an insulative acclimatization. The variation is possibly brought about by a change in an homeostatic mechanism that balances cell production and cell loss.

INTRODUCTION

Since the middle of the nineteenth century, it has been known that in early summer Capercaillie Tetrao urogallus, Black Grouse Lyrurus tetrix, Hazel Hen Tetrastes bonasia, Rock Ptarmigan Lagopus mutus, and Willow Grouse Lagopus lagopus lose the papillae that form a comb-like fringe at the sides of the digit (Meves 1860, Lönnberg 1926, 1927) and the claws get shorter (Nilsson 1935:100, Lönnberg 1926, 1927, Stresemann 1927-34:12, Salomonsen 1939:56-60). In late summer or early autumn, the papillae and the claws successively grow larger to attain the winter size. Lönnberg related the seasonal variation in skin structures to seasonal differences in habits, and thus due to differences in wear. But it can also be argued that the longer papillae and claws in the winter increase the distance between a cold substrate and the living tissues of the digit, which means a more efficient insulation against low temperatures.

Observations on the horny layer of the foot papillae, related to thermoregulation, were made by Madsen & Wingstrand (1959). The papillae in Raven Corvus corax, Snowy Owl Nyctia scandiaca, and Rock Ptarmigan, shot during the arctic winter at Greenland, were studied in histological slides. In the Raven, the horny layer was very

thick, about 2 mm. The opposite, a thin horny layer only 0.2-0.4 mm, was found in a Raven living at the Canary Islands. They concluded that the thick horny layer increased the insulation and prevented injury by frost to the deep lying tissues in the arctic birds.

The aim of the present study is to demonstrate the occurrence of seasonal variation in the foot papillae in one further species of the Galliformes, the Pheasant Phasianus colchicus, and two species of other bird orders, the Wood Pigeon Columba palumbus and the House Sparrow Passer domesticus.

MATERIAL, METHODS, AND TERMINOLOGY,

Wood Pigeons were shot by hunters in Southwest Scania in 1967. The collection was managed by Lars Ljunggren, who studied reproduction and endocrine organs of Wood Pigeons in wood and rural districts (Ljunggren 1968, 1969). In the spring, 147 Wood Pigeons were shot during six periods from 7 February to 11 May (Fig. 4); in the autumn, 61 adult and 53 juvenile Wood Pigeons were shot during four periods from 1 August to 29 September, and 11 juveniles during four periods from 6 October to 28 November (Fig. 5). In each bird in Periods III-X, the structures in the papillae were compared with the reproductive state, as determined by Ljunggren. Values of air temperatures in 1967 and mean month temperatures were obtained from the geographical institute at the University of Lund.

Male Pheasants were shot by hunters in six districts of Sweden (Fig. 1). They were collected in four periods in 1965: April-May, June, August-September, and December (Table 1). The primary purpose was to determine the degree of mercury contamination in Pheasant in 1965, which was the last year that methyl mercury compounds were allowed as seed dressing agency an agriculture in Sweden. The work was conducted by Håkan Stenram and Stig Tejning at the University of Lund. Originally, these were more than 400 birds, but bad fixation or oblique cutting on the microtome reduced the number suitable for measurements to 335.

House Sparrows were collected at Lund in September 1968 and February 1969, 25 specimens on each occasion.

The feet were fixed in Bouin's mixture or a mixture of 80 per cent alcohol, concentrated formol, and concentrated acetic acid in the proportions 18:1:1. After washing in 80 per cent alcohol, the pads were transferred to tetrahydrofuran embedded in paraffin, sectioned at 7 μ m on a rotatory microtome, stained with Ehrlich's haematoxylin and eosin, and mounted in Canadian balsam.

The pads of Wood Pigeon, Pheasant, and House Sparrow are described in earlier studies (p. 21, 81). Pad II:2/3 was measured in the Wood Pigeons, but if the microtome sections on this pad in both the left and right foot were oblique and not

suitable for measurements, pad II:3 was used. Pad IV:4/5 was measured in the Pheasants. The House Sparrow has twelve phalanx pads, and eight of them were measured in the September birds; namely pad I:2, II:2, II:3, III:2, III:3, IV:2, IV:3, and IV:4. In the February birds, only pad I:2 and pad IV:4 were studied.

Fig. 2 shows the general anatomy and terminology of the papilla structures. The general morphology of the blood vascular system in the papilla is based on the work by Vollmerhous & Hegner (1963).

As shown in Fig. 2, three measurements were made in each papilla. The horny layer was measured from the junction of germinative and horny layer to the surface of the papilla; the germinative layer, from an imaginary line between the deep part of germinative layer to the junction between germinative and horny layer; and the secondary dermal papilla, from the deep part of germinative layer to the top of the secondary dermal papilla.

Several secondary dermal papillae were measured in each papilla, and a mean was calculated. In each pad, measurements were carried out on at least five and usually 10-20 papillae from which a mean for that pad was calculated. The House Sparrow has small papillae with few secondary dermal papilla, and it was impossible to get a reliable mean on the length of secondary dermal papillae.

RESULTS

Wood Pigeon

In most of the year, the papillae are pointed structures; but in late April and early May, the papillae in many birds look as if they are worn down to the base. The surface of the pad may be almost smooth.

The histological sections showed that the naked eye evidence is only one part of a process that extends over several months in the spring. The diagrams in Fig. 3 show the normal condition in mid February, mid March, late April, and early May. The horny layer and germinative layer decreased in thickness and the secondary dermal papillae shortened.

The measurements on horny layer, germinative layer, and secondary dermal papillae are shown in Fig. 4 as means, confidence interval of means, and range of variation for each period in the spring. Analysis of variance was applied and the significant differences are indicated in the figure.

The horny layer decreased from 0.21 mm in February to 0.11 mm in early May, the germinative layer from 0.52 mm to 0.40 mm, and the secondary dermal papillae shortened from 0.10 mm to 0.06 mm.

The most distinctive differences in papilla structure are those between period II in early March and period III in late March, when the three parameters decreased

comparatively strongly. This is obviously related to the background history of the birds. The Wood Pigeons in period I and period II were shot in two districts in West Scania, where there was a small wintering population, before the arrival of migrant Wood Pigeon, whereas those in period III were shot in other districts where no Wood Pigeon had wintered.

The species is sedentary for most of its range, e.g., the British Isles and the Netherlands (Troostwijk 1964, Murton 1965), but the majority of Scandinavian pigeons are migratory with departure in late September - mid October and arrival in March - April. The principle wintering districts are those grown with oak woods (Quercus ilex and Q. suber) on the Iberian Peninsula (Troostwijk 1964, Rendahl 1967).

Adult Wood Pigeons were collected in four autumn periods in August - September. The measurements on the papillae are compiled in Fig. 5.

The horny layer was about 0.10 mm in early August; there was no appreciable change compared with early May. In late September, the horny layer had not increased. The germinative layer was about 0.40 mm in August and early September, as in early May; it increased to about 0.46 mm in late September. The secondary dermal papillae were about 0.05 mm in August and early September; they increase to about 0.07 mm in late September.

Thus both the germative layer and the secondary dermal papillae increased from early September to late September. This was the first sign of a change from the papilla structure in the summer to that in the winter.

The juvenile Wood Pigeons were treated separately from the adult. Fig. 5 shows the measurements. The birds in period VIII, late August, had all three measures on average less than the birds of the proceeding period. If the Wood Pigeons in period VIII are disregarded, there was no all over increase in the papilla measurements during the first part of autumn, August-September. In the later part of autumn when most Wood Pigeons had migrated, only a few specimens were shot. The pigeons in October - November (N=11) were compared with the earlier pigeons in August - September (N=42). Between these two groups, the difference in each of the three measurements was significant. The horny layer was about 0.10 mm in early autumn and about 0.16 mm in late autumn ($P < 0.05$); the germinative layer, 0.38 and 0.42 mm ($P < 0.25$); and the secondary dermal papillae, 0.060 and 0.075 mm ($P < 0.05$). Thus, the juveniles in late autumn showed an increase in horny layer and secondary dermal papillae.

The environmental temperature is the most obvious factor that the seasonal variation in papilla structure could be adapted to. Therefore the mean daily temperature in 1967 (mean of the temperatures at 07, 13, and 19 hr) and the normal temperatures in 1931-1960 were studied. There is no good correlation between the prominent changes in air temperature in the spring or in the autumn 1967 and the

changes in papilla structure, either with a time lag of a few days or one or two weeks. The birds were not synchronized to reveal any correlation with temperature. The normal temperature rises gradually from 0°C in mid February to 10°C in mid May; it sinks from 15°C in early September to 7°C in late October. There is a good correlation between the seasonal variation in papilla structure and this seasonal variation in air temperature.

The breeding season of Wood Pigeon in Scania covers 5-6 months in April to September. It could be asked whether the seasonal variation in papilla structure is adapted to the reproductive condition. As the endocrine organs were examined by Ljunggren, a comparison was possible. This examination was performed on the birds in periods III-X. In the spring, the reproductive condition of males was assessed from the weight of testes and the spermatogenesis, as studied in histological sections of testis. The reproductive condition of females was assessed from the diameter of the two largest follicles, the weight of oviduct, and the secretion in oviduct as seen in histological sections. Analyses of variance of different designs on the spring birds were performed, but it was impossible to find any correlation between horny layer, germinative layer, or secondary dermal papillae and the reproductive condition, either in the males or the females. In late September, the gonads were regressed and the change from breeding to non-breeding condition was completed. The germinative layer and the secondary dermal papillae showed significant increase from period IX to period X, but there was no change in the horny layer. The structural condition of the February and March birds had not been achieved when the breeding season ended in September. Thus, the variation in papilla structure in Wood Pigeon was not correlated with the development or the regression of the reproductive system.

The horny layer, germinative layer, and secondary dermal papillae were measured in the papillae of the same pad, and it is natural to suppose that they are related to each other. Therefore the correlations and partial correlations between the measurements were calculated for birds in each period.

The following symbols for measurements were used: a - horny layer, b - germinative layer, and c - secondary dermal papillae. The relations are a - b, a - c, and b - c; the correlation coefficients are r_{ab} , r_{ac} , and r_{bc} ; the partial correlation coefficients are $r_{ab.c}$, $r_{ac.b}$, and $r_{bc.a}$. The values for the spring periods are compiled in Fig. 6.

In Periods I - II and in Periods V - VI, the relations between the parameters were similar. There were positive and significant correlations in the relations a - b, a - c, and b - c. The partial correlation $r_{ab.c}$, however, was close to zero, and the partial correlations $r_{ac.b}$ and $r_{bc.a}$ were equal to or larger than 0.5. This means that the correlation between a and b depended on both structures being correlated with c. In other words, when the horny layer was thick, the germinative

layer also was thick and the secondary dermal papillae were long, but the correlation between horny layer and germinative layer depended on both structures being correlated to the secondary dermal papillae. This suggested that the secondary dermal papillae was the independent factor.

In period III, the relation between the structures were altered. There was no significant correlation in the relations a - b, a - c, or b - c, but $r_{ab.c}$ was positive and significant and $r_{ac.b}$ was negative and significant; $r_{bc.a}$ was not separated from zero. This meant in other words, that when the horny layer was thick, the secondary dermal papillae were short, and this relation was not affected by the size of the germinative layer. This suggests that the change from winter to summer structure was initiated in Period III, late March, by a reduced length of secondary dermal papillae.

The coefficients were also calculated for the adult birds in the autumn periods. As the number of birds in each period was only 9-12, many coefficients were not statistically separated from zero. The correlation coefficients in the three relations a - b, a - c, and b - c were $0.4 < r < 0.8$. There was no change in the values of correlation coefficients comparable to those in the spring.

Pheasant

The seasonal variation in papilla structure of the Pheasants could not be recognized by a macroscopic examination of the sole. The papillae were low and flat throughout the year.

The measurements of horny layer, germinative layer, and secondary dermal papillae are shown in Table 1 as mean and confidence interval of mean for each parameter, period, and locality. The probability for difference between localities is indicated. Fig. 7 shows the mean values for the period.

The horny layer, germinative layer, and secondary dermal papillae showed the highest values in December and the lowest values in June. In April-May, the germinative layer and secondary dermal papillae were reduced to near the June condition, but the horny layer was intermediate between December and June. In August-September, the values had increased slightly compared with June.

The thickness of horny layer varied on average from 0.52 to 0.22 mm in December and June; the highest locality mean was 0.59 mm and the lowest 0.20 mm. The germinative layer varied proportionally less than the horny layer, from 0.58 to 0.41 mm. The secondary dermal papillae ranged from 0.126 to 0.078 mm.

Between localities, the differences were small in June but great in April-May, particularly concerning the horny layer; the Pheasants at Öved had a horny layer about twice as thick as those at Gryt.

The seasonal variation in papilla structure in Pheasant obviously extended over several months. In the spring, the first changes appeared as a decreased thickness

of germinative layer and a shortening of secondary dermal papillae.

The Pheasants were collected for a study of mercury contamination. Unfortunately it was impossible to compare the degree of contamination, measured in the liver, and the papilla structure in the individual bird. There was very great individual variation in mercury contamination between Pheasants in the same period and the same locality (H. Stenram, personal comm.). The average values for period and locality showed highest concentration of mercury in June after the spring sowing; it had decreased substantially in August - September. The mercury contamination, however, could not account for the seasonal variation, although some individual birds with high concentration might have been in a bad condition.

House Sparrow

Adult House Sparrows were collected in early September, when the air temperature even at night was above $+7^{\circ}\text{C}$, and in late February, when the air temperature for a longer period was below zero, even during the day. The horny layer was on average 0.15 mm in the summer birds and 0.19 mm in the winter birds; the germinative layer was 0.47 mm and 0.53 mm, respectively. Both pairs of mean values are significant ($P < 0.01$).

DISCUSSION

The seasonal variation in the structure of the foot papillae of Wood Pigeon, Pheasant, and House Sparrow is clearly the same phenomenon that has earlier been observed to occur in the comb-like row of papillae in the digits of grouse (see 'Introduction'), The changes are a slow process extending over several months.

In the Wood Pigeon, the structural changes in spring are initiated by a shortening of the length of secondary dermal papillae. The length of the secondary dermal papillae can be regarded as an expression of the area of contact between dermis and epidermis, or the number of basal epidermal cells. The reduced length of secondary dermal papillae implies a reduced number of basal cells, which are the site of mitotic activity.

The homeostatic mechanism that maintains the epidermis at a particular thickness has not been studied in birds, but much is known from studies on mammalian epidermis (short review with further references by Bullough 1970). The hypothesis proposed by Bullough states that the principle control of the mitotic activity resides within the tissue, and the control mechanism appears to operate through an inhibition of mitosis by a tissue-specific inhibitor, a glycoprotein, that has been isolated and termed epidermal chalone. There is evidence that the chalone concentra-

tion in germinative layer maintains the balance between cell production and cell loss. The chalone action is strengthened by the presence of adrenalin. When during stress the chalone efficiency is higher, the mitotic activity is reduced, but the epidermis does not become thinner because the transition of cells from germinative to horny layer is also reduced by action of the chalone. On the contrary, when the production of epidermal cells is increased by high mitotic activity, the transition of cells from germinative to horny layer is also high, but the thickness of epidermis is maintained at the normal level. These circumstances indicate that the loss of horny cells from the surface is not merely an effect of wear, but also involves an active process.

From the evidence on mammalian epidermis, the seasonal variation in the foot papillae of birds cannot be understood as a simple effect of wear. It is more probable that the variation is brought about by changes in an homeostatic mechanism.

The seasonal variation in papilla structure might be an adaptation to the seasonal variation in environmental temperature and the adaptive significance might concern the peripheral thermoregulation.

The appendages are an important part in the thermoregulatory system of birds, both for the dissipation of excessive heat and for the conservation of heat during thermal stress (reviews by King & Farner 1961, Dawson & Hudson 1970). The capacity to keep the leg temperature substantially below the body temperature is achieved by a system of counter current heat exchange by which the heat in the descending arterial blood is cooled by the returning venous blood. The part of the vascular system working in this exchange is supposed to lie deep in the shank, where the major artery is accompanied by one or several veins (Scholander 1955, Irving & Krog 1955, Kahl 1963, Steen & Steen 1965). This mechanism keeps the peripheral part of the leg at a low temperature. In a study of cold-adapted Pheasants at ambient temperatures of -18°C , the temperature in the shank ranged from $+7^{\circ}\text{C}$ to $+10^{\circ}\text{C}$, and in the dermis of the distal part of the digit, it was $+2.7^{\circ}\text{C}$ (Elderstrom & Brumleve 1964). When an animal is exposed to temperatures below the tissue freezing temperature, the counter current exclusion of heat could cause freezing unless there was some other mechanism to maintain the temperature of the living cells in dermis and epidermis above the tissue freezing point. Such a mechanism has been shown to operate in the foot pad of arctic fox Alopex lagopus and gray wolves Canis lupus (Henshaw, Underwood & Casey 1972). The foot have cutaneous vascular plexus of blood vessels. These, during extremely low ambient temperatures, stabilize by selective shunting the subcutaneous temperature with great precision just above freezing point, -1°C with largest deviation -0.7°C . Arterio-venous anastomoses have been demonstrated in the deep part of the primary

dermal papilla in the foot of domestic hen (Vollmerhaus & Hegner 1963), and this might be the structural basis for a similar mechanism in birds.

The heat flow in the papilla is affected by the heat flow in the blood vessels that penetrate into the primary dermal papilla by arterioles and venules and to the top of the secondary dermal papillae by capillaries as indicated in Fig. 2. From the top of the secondary dermal papillae to the surface, the heat flow occurs by thermal conduction, which is the general way of heat transfer in epidermis (Birkebak 1966, Tregear 1966). At the surface, the heat may be lost to the environment by conduction, convection, or radiation. In the resting bird, the papillae have intimate contact with the substrate, and the heat is probably transferred from one conductive medium (epidermis) to another (substrate). The heat transfer may be supposed to occur mainly through the papillae and only to a minor extent via the small volumes of air between the papillae.

In a homogeneous and isotropic conductive material, the heat flow is proportional to the temperature gradient and the surface, according to the physical law of heat conduction first stated by Fourier and expressed by the equation $\underline{H} = -k A \frac{dt}{dx}$, where $\underline{H}$ is the rate of heat flow, k is the proportionality constant or thermal conductivity which depends on the nature of the material, $\underline{A}$ is an area perpendicular to the heat flow direction, and $-\frac{dx}{dt}$ is the temperature gradient in x -direction, which is measured from higher to lower temperature, from deep core to surface. The tissues of foot papilla may be supposed in an approximate way to obey the Fourier's equation. If the temperature in the deep part of dermis (T_d) and the temperature at the surface of papilla (T_s) are constant in a system of steady state, the equation can be integrated to: $\underline{H} = k A (T_d - T_s) / L$, where $\underline{L}$ is the thickness of the conducting layer. The increased thickness of the germinative layer and particularly of the horny layer in winter implies a reduced rate of heat flow.

In winter, the Wood Pigeon (Fig. 5) and House Sparrow have more pointed papillae with minor flat top surface. This indicates that the surface of contact with the substrate is less in winter than in summer. If Fourier's equation is valid, the factor $\underline{A}$ is changed, and this also means a reduced rate of heat flow.

A number of birds resident in temperate climates are able to make metabolic and insulative changes, which are referred to as acclimatization (Hart 1957, West 1962, Helms 1968). The insulative acclimatization (insulation $\underline{I} = L / k$) means a change in the overall insulation and/or vasomotor responses in the blood vascular system. The occurrence of this acclimatization has been deduced principally from the studies on the relation between metabolic rate and ambient temperature in summer and in winter. This relation has been shown to change from summer to winter in Yellow

Bunting Emberiza citrinella (Wallgren 1954), Cardinal Richmondia cardinalis, (Dawson 1958), and Willow Ptarmigan (West 1972a), but similar changes could not be confirmed in other species, i.e. in Redpoll Carduelis flammea (West 1972b)

The lower limit of temperature tolerance has also been shown to change by season, indicating the occurrence of acclimatization. The House Sparrow extends the lower limit of temperature tolerance from 0°C in summer to -35°C in winter (Barnett 1970). There is a gradual loss of tolerance in the spring, $3^{\circ}\text{C}/\text{month}$, which is associated with a gradual loss of body feathers, a decrease in fat reserves, and a lower metabolic rate in muscle and brain tissue. In the autumn, the gain in tolerance is $6^{\circ}\text{C}/\text{month}$, but the increase is more rapid in connection with the autumnal moult, when the body feathers increased by 70 per cent.

The feathers participate in the insulative acclimatization. In the House Sparrow, the weight of feathers increases by 29 per cent from summer to winter (Kendeigh 1934:334); in the Tree Sparrow Spizella arborea it increases by 25 per cent (West 1960). A seasonal variation in the number of feathers is obviously a common phenomenon in resident temperate birds (Wetmore 1936), but the variation in the number of feathers is far less than that in the number of hairs or thickness of fur in mammals (Irwing 1960). It depends largely on the function of feathers in forming a smooth surface suitable for flight.

The physiologically recorded insulative acclimatization could thus be due to changes in the quantity of feathers, but evidence in the present study indicates that the changes in the structure of foot papillae also contribute to the acclimatization.

LITERATURE

- Barnett, L.B. 1970. Seasonal changes in temperature acclimatization of the House Sparrow Passer domesticus. - Comp. Biochem. Physiol. 33:559-578.
- Birkebak, R.C. 1966. Heat transfer in biological systems. Pp. 269-344 in Felts, W.J.L. & Harrison, R.J. (eds.): International Review of General and Experimental Zoology, Vol. 2. Academic Press, New York & London.
- Bullough, W.S. 1970. The rejuvenation of the skin. - J. Soc. Cosmet. Chem. 21:503-520.
- Dawson, W.R. 1958. Relation of oxygen consumption and evaporative water loss to temperature in the Cardinal. - Physiol. Zool. 31:37-48.
- Dawson, W.R. & Hudson, J.W. 1970. Birds. Pp. 223-310 in Whittow, G.C. (ed.): Comparative Physiology of Thermoregulation. Academic Press, New York & London.
- Ederstrom, H.E. & Brumleve, S.J. 1964. Temperature gradients in the legs of cold-adapted pheasants. - American Journ. Physiol. 207:457-459.
- Hart, J.S. 1957. Climatic and temperature induced changes in the energetics of homeotherms. - Rev. Canad. Biol. 16:133-174.
- Helms, C.W. 1968. Food, fat, and feathers. - Amer. Zool. 8:151-167.
- Henshaw, R.E., Underwood, L.S., and Casey, T.M. 1972. Peripheral thermoregulation: foot temperature in two arctic canines. - Science 175:988-990.
- Irving, L. 1960. Birds of Anaktuvuk Pass, Kobuk, and Old Crow. A study in arctic adaptation. - U.S. Nat. Mus. Bull. 217:1-409.
- Irving, L. & Krog, J. 1955. Temperature of skin in the arctic as a regulator of heat. - Journ. Applied Physiol. 7:355-364.
- Kahl, M.P. 1963. Thermoregulation in the Wood Stork, with special reference to the role of the legs. - Physiol. Zool. 36:141-151.
- Kendeigh, S.C. 1934. The role of environment in the life of birds. - Ecol. Monogr. 4:299-417.
- King, J.R. & Farner, D.S. 1961. Energy metabolism, thermoregulation and body temperature. Pp. 215-288 in Marshall, A.J. (ed.): Biology and Comparative Physiology of Birds. Academic Press, New York & London.
- Ljunggren, L. 1968. Seasonal studies of Wood Pigeon populations. I. Body weight, feeding habits, liver and thyroid activity. - Viltrevy 5:435-504.
- Ljunggren, L. 1969. Seasonal studies of Wood Pigeon populations. II. Gonads, crop glands, adrenals and the hypothalamo-hypophysial system. - Viltrevy 6:41-126.
- Lönnberg, E. 1926. Några bidrag till kännedomen om våra skogshöns, Tetraonidae. - Fauna och Flora 21:241-255.
- Lönnberg, E. 1927. Einige Beiträge zur Kenntnis unserer Waldhühner, Tetraonidae. - J. Ornithol. 75:579-596.
- Madsen, H. & Wingstrand, K.G. 1959. Some behavioural reactions and structures enabling birds to endure winter frost in arctic regions. - Vidensk. Meddel. Dansk Naturh. Foren. 120:15-23.
- Meves, W. 1860. Bidrag till Jemtlands Ornitologi. - Öfversikt av Kongl. Vetenskaps-akademiens Förhandlingar 17:137-224.
- Murton, R.K. 1965. The Wood Pigeon. Collins, London.
- Nilsson, S. 1835. Skandinavisk Fauna. Foglarna. Vol. 2. Berlingska Boktryckeriet, Lund.

- Rendahl, H. 1967. Die Zugverhältnisse der schwedischen Ringeltauben (Columb palumbus L.) und Hohltauben (Columba oenas L.). - Arkiv för Zoologi 18:221-266.
- Salomonsen, F. 1939. Moults and sequence of plumages in the Rock Ptarmigan (Lagopus mutus (Montin)). - Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening. Vol. 103:1-491.
- Scholander, P.F. 1955. Evolution of climatic adaptation in homeotherms. - Evolution 9:15-26.
- Stresemann, E. 1927-34. Aves. In: Klüppenthal, W. & Krumbach, T. (eds.). Handbuch der Zoologie, Vol. 7:2. Wied. Gruyter, Berlin & Leipzig.
- Steen, I. & Steen, J.B. 1965. The importance of the legs in the thermoregulation of birds. - Acta Physiol. Scand. 63:285-291.
- Tregear, R.T. 1966. Physical Functions of Skin. Academic Press, London & New York.
- Troostwijk, W.J.D. van. 1964. Some aspects of the Woodpigeon population in the Netherlands. - Ardea 52:13-29.
- Vollmerhaus, B. & Hegner, D. 1963. Korrosionsanatomische Untersuchungen am Blutgefäßsystem des Hühnerfusses. - Morph. Jahrb. 105:139-184.
- Wallgren, H. 1954. Energy metabolism of two species of the genus Emberiza as correlated with distribution and migration. - Acta Zool. Fenn. 84:1-110.
- West, G.C. 1960. Seasonal variation in the energy balance of the tree sparrow in relation to migration. - Auk 77:306-329.
- West, G.C. 1962. Responses and adaptations of wild birds to environmental temperature. Pp. 291-333 in Hannon, J.P. & Viereck, E. (eds.): Comparative Physiology of Temperature Regulation. Arctic Aeromed. Lab., Ft. Wainwright, Alaska.
- West, G.C. 1972a. Seasonal differences in the resting metabolic rate of Alaskan ptarmigan. - Comp. Biochem. Physiol. 42A:867-876.
- West, G.C. 1972b. The effect of acclimation and acclimatization on the resting metabolic rate of the common redpoll. - Comp. Biochem. Physiol. 43A:293-310.
- Wetmore, A. 1936. The number of contour feathers in passeriform and related birds. - Auk 53:159-169.

Table 1. Horny layer, germinative layer, and secondary dermal papillae in male Pheasants, shot during four periods in 1965. The figures are mean for local and period, and 95 per cent confidence interval for mean. The number investigated for each local and period are shown at the figures for horny layer; the same number was used for germinative layer and secondary dermal papillae. Analysis of variance was performed on each measure within period, and the probability for difference between locals is indicated.

111

Locality	20 April - 12 May			17 - 20 June			18 August - 13 September *			3 - 20 December		
	Mean	Conf. int.	No.	Mean	Conf. int.	No.	Mean	Conf. int.	No.	Mean	Conf. int.	No.
<u>Horny layer</u>												
Öved	.48	.45- .51	20	.22	.21- .24	20	.26	.24- .27	23	.59	.55- .62	20
Gryt	.27	.25- .30	15	.20	.18- .22	15	.26	.23- .28	8	.49	.45- .53	15
Halltorp	.34	.29- .39	14	-	-	0	-	-	0	.57	.53- .61	24
Alvesta	.42	.37- .47	12	.23	.21- .25	15	.27	.24- .30	8	.53	.50- .55	20
Asker	.37	.33- .40	11	.24	.20- .27	7	.23	.19- .28	5	.50	.47- .52	22
Ballingsta	.38	.36- .40	16	.21	.20- .23	14	.27	.25- .30	8	.50	.48- .62	23
test	P < .001			P < .1			P > .25			P < .001		
<u>Germinative layer</u>												
Öved	.50	.47- .53		.41	.39- .44		.50	.47- .53		.50	.48- .53	
Gryt	.42	.39- .45		.43	.39- .46		.44	.38- .50		.55	.53- .58	
Halltorp	.43	.40- .46		-	-		-	-		.63	.60- .65	
Alvesta	.53	.48- .57		.46	.42- .49		.55	.46- .64		.62	.59- .65	
Asker	.47	.42- .53		.40	.34- .46		.44	.35- .53		.57	.53- .60	
Ballingsta	.49	.45- .53		.42	.38- .47		.52	.45- .58		.60	.58- .62	
test	P < .001			P > .25			P ~ .05			P < .001		
<u>Secondary dermal papillae</u>												
Öved	.098	.091- .105		.086	.080- .092		.086	.080- .092		.128	.117- .139	
Gryt	.073	.065- .081		.080	.070- .090		.077	.059- .095		.127	.117- .137	
Halltorp	.063	.057- .070		-	-		-	-		.128	.122- .134	
Alvesta	.092	.081- .103		.083	.076- .090		.098	.087- .105		.143	.132- .154	
Asker	.093	.075- .111		.079	.073- .085		.076	.068- .084		.119	.111- .127	
Ballingsta	.076	.067- .085		.061	.050- .072		.080	.067- 0.93		.109	.102- .116	
test	P < .001			P < .001			P < .1			P < .001		

* Asker: 20-28 September



Fig. 1. Six districts in Sweden where collection of Pheasants was carried out in 1965.

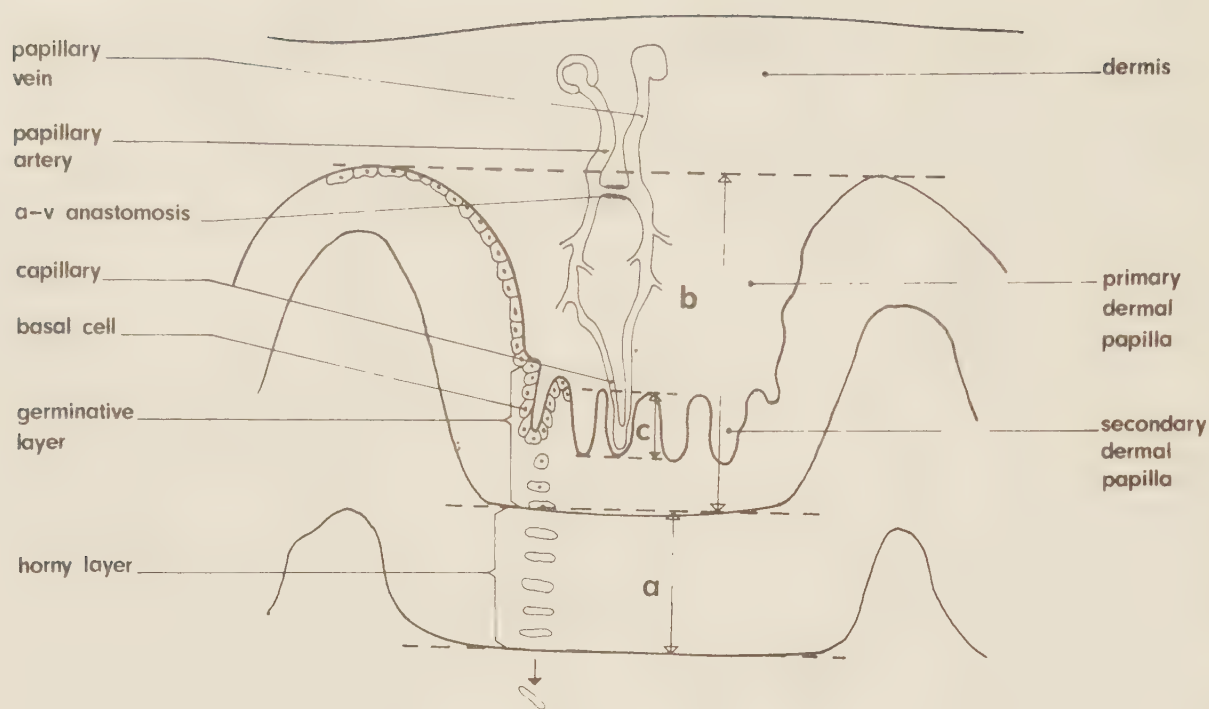


Fig. 2. The general anatomy and terminology of the papilla and the way of measuring (a) horny layer, (b) germinative layer, and (c) secondary dermal papillae.

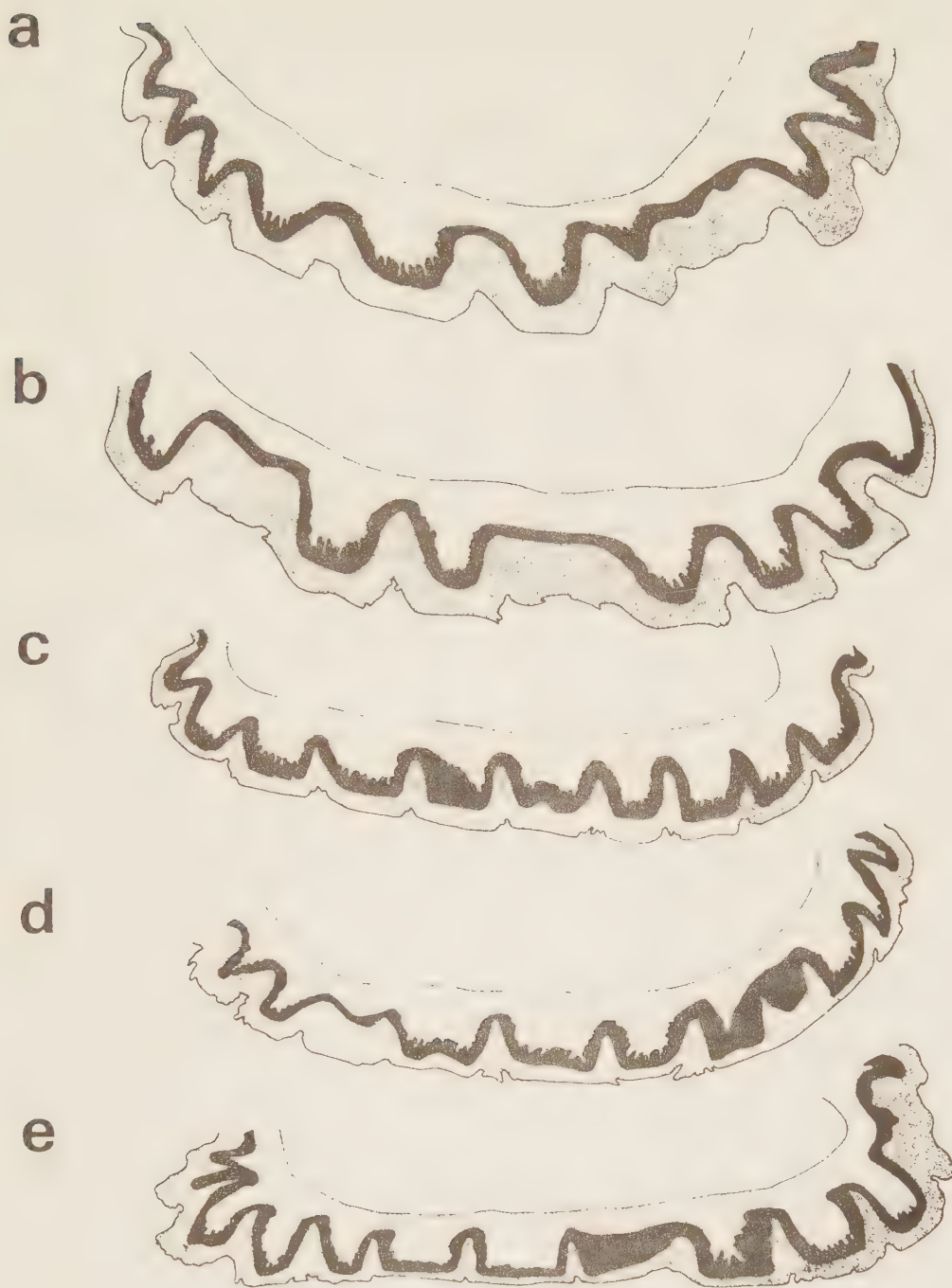


Fig. 3. Structure of Wood Pigeon papillae in (a) a mid February bird, (b) a mid March bird, (c) a late April bird, and (d) and (e) early May birds. Halftone area indicates horny layer; black area, germinative layer; spotted area, dermis. The diagrams show the decreasing thickness of horny layer and germinative layer and the shortening of secondary dermal papillae by the advancing spring.

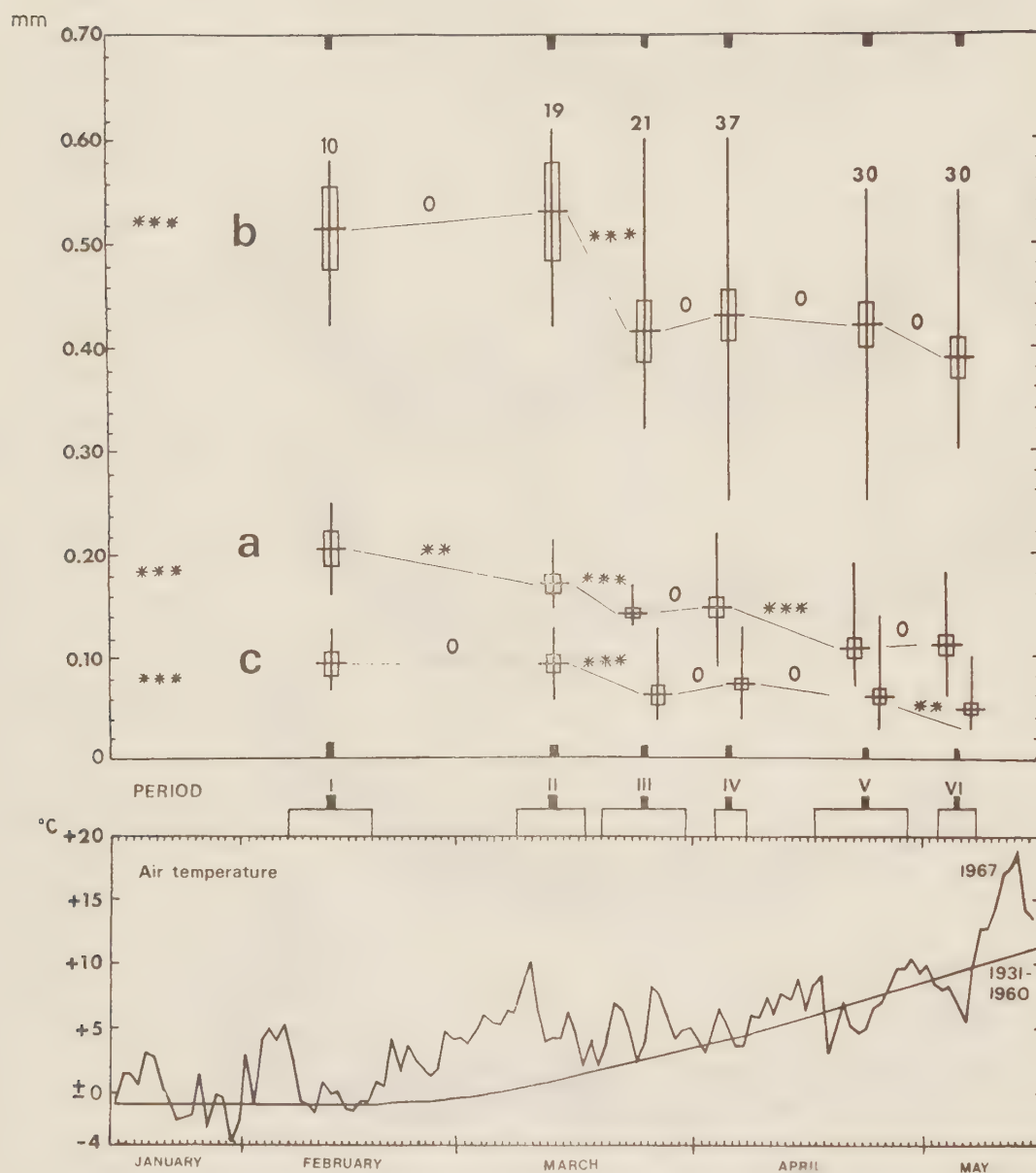


Fig. 4. Seasonal variation in (a) horny layer, (b) germinative layer, and (c) secondary dermal papillae in Wood Pigeons, collected during six spring periods in 1967. Vertical scale in millimetres. The period lengths are indicated on the basis of the diagram. Number of investigated birds, mean value, 95 per cent confidence interval of mean, and range of variation are shown for each period. Analysis of variance was applied: (i) on all periods simultaneously, probability for difference indicated by asterisks to the left of letters a, b, and c; (ii) on two close periods, asterisks between the means. 0 indicates $P > 0.05$; *, $P < 0.05$; XX, $P < 0.01$; XXX, $P < 0.001$.

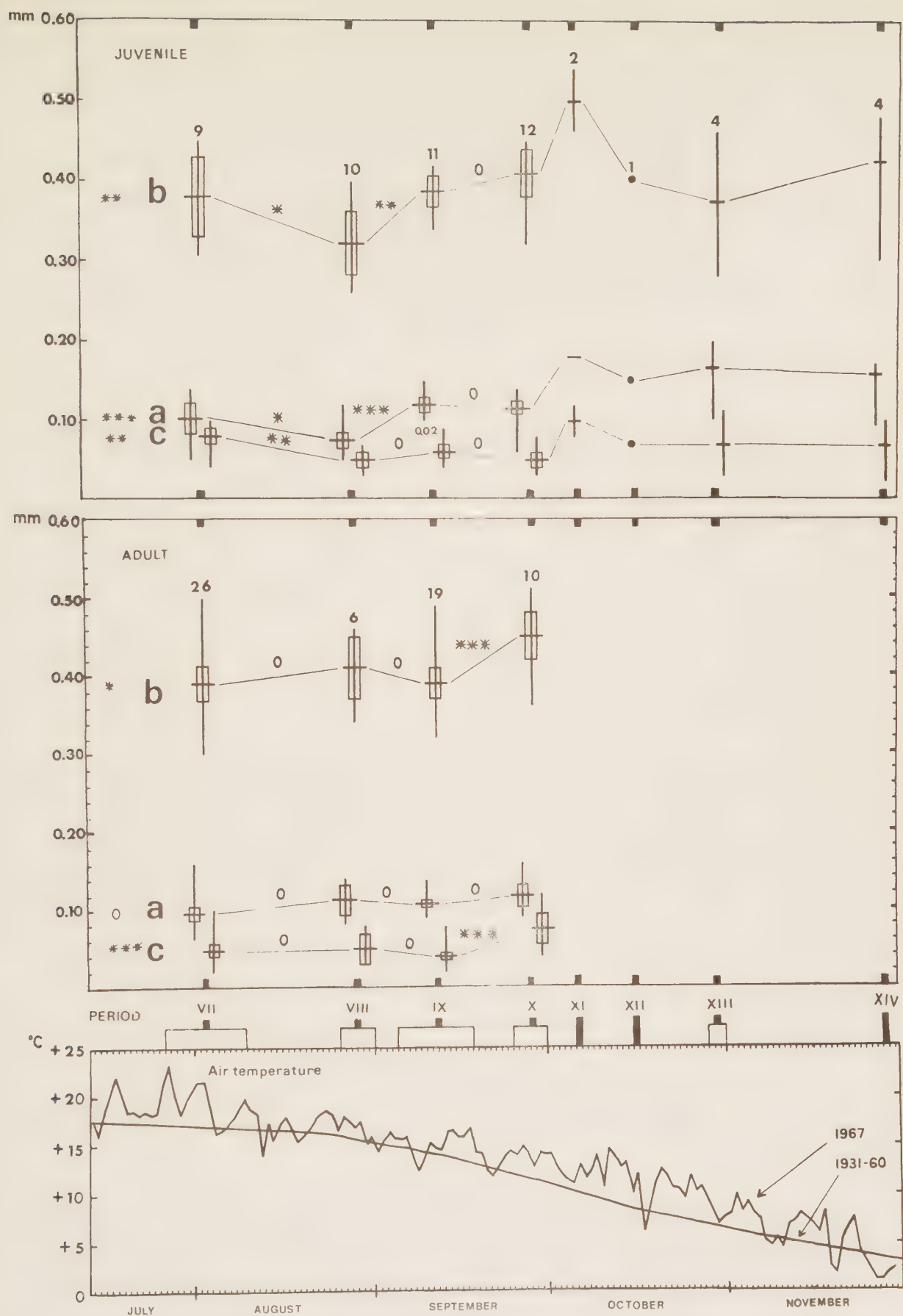


Fig. 5. Seasonal variation in (a) horny layer, (b) germinative layer, and (c) secondary dermal papillae in juvenile and adult Wood Pigeons, collected during eight autumn periods in 1967. Vertical scale in millimetres. Symbols and other explanations as in Fig. 4.

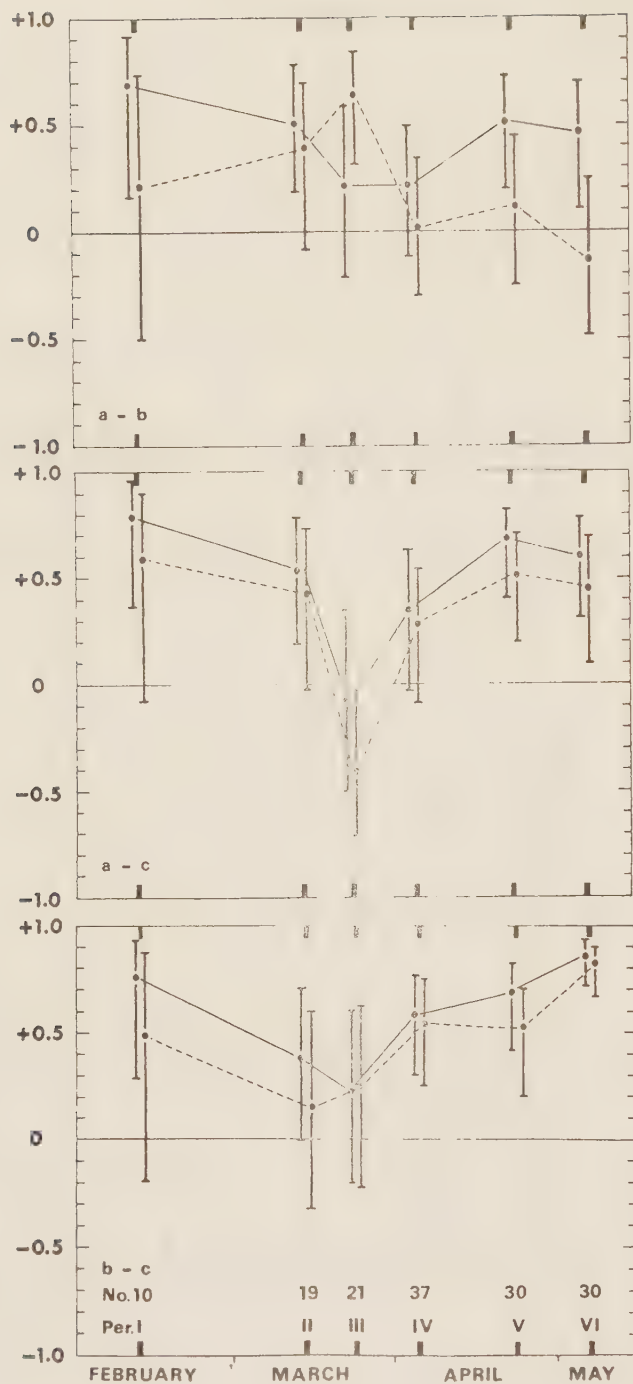


Fig. 6. Correlations and partial correlations between the structures in the papillae of Wood Pigeon in six spring periods. The structures correlated are: a - horny layer, b - germinative layer, and c - secondary dermal papillae. Upper diagram shows the correlation coefficients r_{ab} , connected by continuous lines; the partial correlation coefficients $r_{ab.c}$, connected by broken lines; 95 per cent confidence interval of the coefficients, vertical lines. The middle diagram shows correspondingly the coefficients r_{ac} and $r_{ac.b}$, and the lower diagram, the coefficients r_{bc} and $r_{bc.a}$.

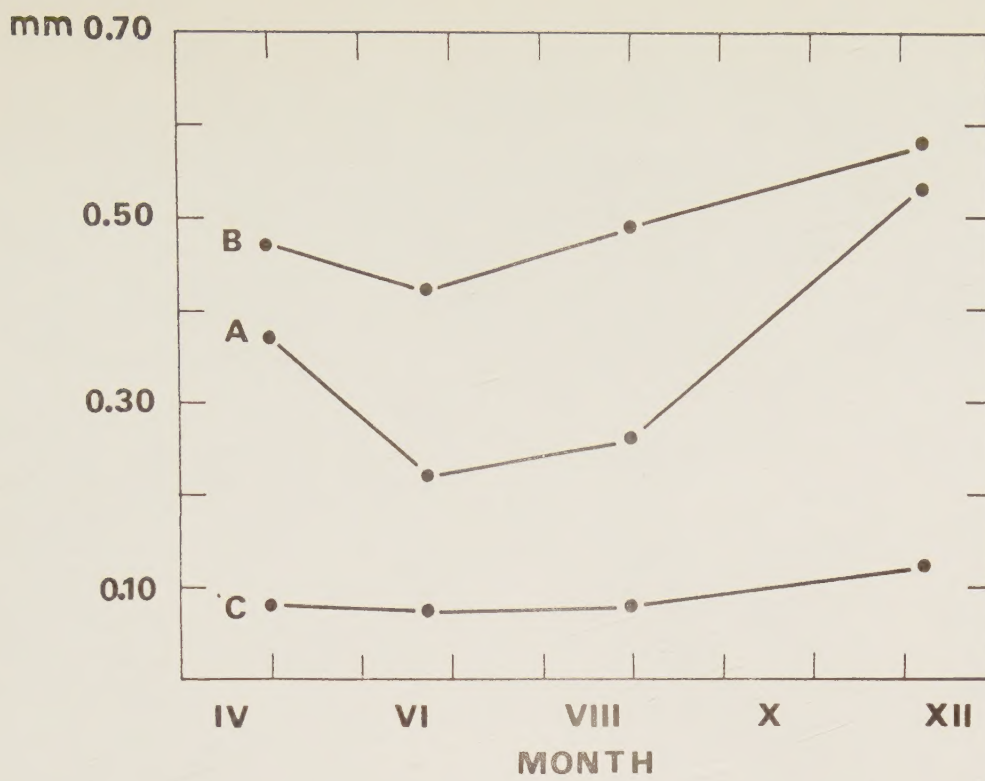


Fig. 7. Seasonal variation in (a) horny layer, (b) germinative layer, and (c) secondary dermal papillae in male Pheasants shot during four periods in 1965. The values are calculated as means of five or six local mean values compiled in Table 1.

